VI. The Entomophthoreae of the United States.

By Roland Thaxter.

THE material upon which the following account is based was accumulated, for the most part, during the seasons of 1886–7, from several localities in New England and in North Carolina, which were examined with such thoroughness as the limited time at my disposal would allow. The New England material was chiefly collected at Kittery Point, Maine, the southernmost point in the state, and in the vicinity of Boston; while the remainder is the result of two weeks botanizing in the alpine and sub-alpine region of Mt. Washington, N. H. The more southern forms represent three principal localities in or near the western portion of North Carolina. Of these Cullowhee, 2400 ft. above the sea, is the southernmost, having a flora of a distinctly southern type; while the two others, Cranberry (3250 ft.) and Burbank (E. Tennessee, 3500 ft.), have a climate and flora not unlike that of the southern New England states. The eastern section of the United States is thus fairly well represented in so far as the localities which have been studied are concerned; yet it is scarcely necessary to remark that the forms obtained during a few weeks' sojourn in each locality, in the course of general botanizing, can represent only in a fragmentary way the Entomophthoreae of this section of the country. The forms occurring in the more remote regions of North America are, moreover, as yet almost wholly unknown; and, although my observations have served to increase the number of American representatives from four previously recorded forms to the considerable number hereafter enumerated, it cannot be supposed that the record is other than very imperfect. The present paper is therefore complete only in so far as I have endeavored to combine my own observations with those of previous students of the group in this country and in Europe.

For this purpose the literature of the subject has been consulted as far as has been practicable, and a list of the papers that I have myself seen is appended to this memoir. It should be understood, however, that this list is not intended as a complete record of all that has been written upon the subject, and is merely given for convenience of reference in the text.

The Russian publications of Sorokin were kindly procured for me in St. Petersburg by Mr. Charles Eliot, and for some knowledge of their contents I am indebted to Mr. Ivan Panin. For the privilege of examining the remaining papers, not contained in the University libraries in Cambridge, together with other invaluable assistance, I am indebted to Professor Farlow, in whose laboratory the microscopic work upon my paper has been for the most part done. To Miss Hapgood I owe certain extracts from the Polish of

Nowakowski, and I am also indebted to Professor Farlow, Messrs. C. V. Riley, L. O. Howard, Henry Edwards and A. F. Chatfield for several interesting specimens. To Mr. C. W. Woodworth and Prof. S. W. Williston I also owe certain entomological determinations.

The plants that are to be considered in the present paper belong to a class which, although made up of several groups differing widely from one another in their habit and affinities, is yet, by reason of a peculiarity common to all its members, possessed of a certain individuality of its own that renders it susceptible of a consideration apart from all other forms of plant life. This peculiarity, by reason of which the class is usually characterized as entomogenous or entomophytous, consists in an obligatory parasitism upon insects, which, although in some instances it exists without apparent injury to the insect host, is usually of such a nature as to cause its death; often resulting, especially among noxious insects, in widespread mortality.

Although a few of the more common or conspicuous forms of entomophytous plants had attracted the notice of botanists even in the last century, it was not until within comparatively recent years that they began to be studied with any care, and the work of Robin[1] is the first contribution of importance on the subject. This work still remains, with two exceptions,[2] the only attempt that has been made to bring together all the known forms of insect parasites; but since its publication very important contributions have been made to our knowledge of the subject, through the medium of numerous scattered papers.

My attention was first turned in this direction in the course of entomological studies on the life-histories of certain insects; in the course of which I was often greatly annoyed by losing large numbers of larvae and pupae through the agency of fungi. Having by this means and from other sources accumulated a certain amount of material, it was my first intention to include in my paper all the entomogenous plants recorded from America; yet, owing to the many difficulties presented by the ascomycetous forms, involving a careful study and comparison of more abundant material than I could command, as well as by reason of the considerable additions to our Entomophthoreae resulting from my observations, I have decided to confine myself for the present to the members of this family, trusting to a future opportunity of extending my paper in conformity with my original plan. In the meantime a brief summary of the more important groups may not be out of place in this connection, and will be a fitting introduction to the more detailed consideration of the Entomophthoreae which follows.

Summary of entomogenous plants.—Although the spiders and myriapods are not exempt from the attack of peculiar vegetable parasites, the hexapod insects offer by far the greater number of instances of this nature. Among the seven orders of the latter class usually enumerated, the Neuroptera and Orthoptera are almost wholly free from such attack; and, until recently, the first named order was considered wholly exempt in this respect. Of the remaining orders the Lepidoptera and Diptera are apparently the greatest sufferers; while the Hemiptera, Coleoptera and Hymenoptera are about equally af-

[1] C. Robin, *l. c.*

[2] Sorokin, *l. c.*, C, and Gray, G. R: Notices of insects that are known to form the bases of fungoid parasites, London, 1858.

fected. Of the different stages of insects the imagines, larvae and pupae may all be parasitized, and in some instances a single parasite may attack all these stages in one or more species of the same or different orders; while in others it may confine itself to a single stage or species.

Entomogenous plants may in a general way be referred to five principal groups: one including the bacterial forms which produce disease in insects; a second represented by certain entophytous algae; and three others all belonging to the fungi proper.

The first mentioned group, represented by the Bacteria, is chiefly of interest from an economic, rather than from a botanical point of view, as the supposed cause of destructive epidemics among useful as well as noxious insects. Instances of this kind are presented by the disease known as *flacherie* so destructive to silk worms, and in affections of a similar nature in other insects, where the "active principle" has, in some cases, been traced to bacterial forms which have been considered sufficiently peculiar to receive distinctive names. The systematic study of the group is necessarily one of great difficulty, and any opinion as to the validity of specific distinctions in such cases can only be formed by specialists in this department; but from a practical standpoint the existence of such affections promises to afford an important means of defence against noxious insects.

The second group includes a small number of peculiar filamentous algae, represented by *Enterobryus* and its allies, that live attached to the digestive tracts of certain myriapods and coleopterous larvae. They are apparently nearly related to *Oscillaria* or *Beggiatoa* among the Protophytes; but, owing to insufficient observations upon them, their exact affinities are unknown. Their habit is probably one of commensalism, rather than of true parasitism; the partially digested food of the host being absorbed directly from the digestive tract.[1]

The fungoid parasites of insects are, as before mentioned, represented by three chief groups: the Entomophthoreae, the Laboulbeniaceae and the entomogenous forms which constitute the bulk of the genus *Cordyceps*. Since the first of these is to receive special consideration hereafter, it need only be said that its members are closely allied to the Mucorini among the Zygomycetes, and are entomogenous with few exceptions.

The *Laboulbeniaceae* constitute a small group of very peculiar and minute forms which have been placed by DeBary among the doubtful Ascomycetes. Their parasitism is an external one, which apparently results in little if any inconvenience to the host; each individual being fixed by a pedicellate attachment to the legs, thorax or other portion of the affected insect. Several genera on Diptera, Coleoptera, etc., are described by Peyritsch[2] to whom we are principally indebted for our knowledge of the group, although the first genus of the family (*Laboulbenia*) was described and figured by Robin.[3] The single American representative thus far recorded has been described by Professor Peck as *Appendicularia entomophila*, n.g. et sp.[4]

The pyrenomycetous genus *Cordyceps* affords by far the most conspicuous examples of entomogenous plants, many of which are of large size, or brightly colored, and have

[1] See Leidy, Smiths. Contr. to Knowledge, v, pp. 1–67 (1853) and Robin *l. c.*, p. 395.

[2] Sitz. d. Akad. wiss. Wien., 64, I, p. 441 (1871): 68, I, p. 227 (1873): 72, I, p. 377 (1875), plates.

[3] *l. c.*, p. 622, plates.

[4] Peck, 38th Report, p. 95, with plate.

therefore received more attention from earlier botanists. Their imperfect or "*Isaria*" condition is familiar to all entomologists as a pest in breeding cages and puparia; although the ascigerous condition is usually of rare occurrence. They attack all orders of hexapod insects, larvae and pupae as well as imagines, and also certain spiders; often producing what is vulgarly known as a "vegetable sprout" several inches in length. A considerable number of American species are recorded; yet, owing to the lack of sufficiently well-marked microscopic characters, as well as to the scarcity of good material for study, the group presents many difficulties, as is usual in cases when too great reliance has been placed upon gross characters as a means of specific distinction.

In addition to the groups above mentioned there are several other isolated instances of entomogenous fungi, among which should be mentioned the so-called *Botrytis Bassiana* which produces the disease known as *Muscardine*, so destructive to silk worms in Europe and apparently identical with a similar form occurring in this country.

Facultative parasites of insects.—In addition to the obligate parasites briefly enumerated above, insects are often subject to the attack of numerous small moulds and bacteria which are in no sense peculiar to them, although they may temporarily assume a habit which is practically that of a true parasite, entering the living host and causing its death. It seems also probable that one or two forms which are truly entomogenous are yet saprophytes, as in the case of a certain *Cordyceps* (*C. armeniaca*) presumably growing upon the remains of insects in the excrement of insectivorous birds, as well as the members of the genus *Basidiobolus* hereafter mentioned, which occur upon the excrement of frogs and lizards. DeBary has also pointed out that the species of *Cordyceps* are normally partial saprophytes, since they attain their full development after the death of the host; but whether wholly parasites or saprophytes, or parasites and saprophytes combined, their peculiarity in growing naturally only upon insects or insect remains constitutes them entomogenous, in the sense in which I use the term, to the exclusion of such forms as *Penicillium*, *Aspergillus*, *Cladosporium* and the like; which, although they may at times not only grow on insects, but become temporarily truly parasitic upon them, are yet found in nature on a great variety of other substances.

With this brief reference to entomogenous plants in general we may now turn to the consideration in detail of the group which forms the subject of the present paper.

Entomophthoreae.

General characters.—This family at present comprises several genera, the members of which are not all entomogenous, though closely related structurally. They are distinguished by the production of numerous hyphae of large diameter and fatty contents, which, in the insect forms, ultimately emerge from the host in white masses of characteristic appearance and produce at their extremities large conidial spores which are violently discharged into the air and propagate the disease. The common house-fly fungus is perhaps the most familiar example of the kind, and no one can have failed to notice the affected flies in autumn or late summer adhering to looking-glasses or window-panes surrounded by a smoky halo of discharged conidia. In addition to these conidia the propagation of the fungus, after long periods of rest, may be provided for by the formation of thick-walled resting spores adapted to withstand successfully the most unfavorable conditions. These resting spores, which may be either sexual (zygospores), or asexual (azygospores), finally germinate and produce conidia that are discharged in the usual fashion and serve to infect fresh hosts. Such in brief is the general mode of development in Entomophthoreae; yet it is subject to so many variations and modifications in the different genera and species that a detailed comparison of them is instructive as well as necessary for a sufficient understanding of the family. I shall therefore consider each stage among the *Empusae* in some detail, having first briefly mentioned the more important points of structure in the remaining genera. These genera are four in number: *Completoria*, *Conidiobolus*, *Basidiobolus* and *Massospora*, the members of which, as already mentioned, are not all entomogenous.

The genus Completoria, which, as has been pointed out by Nowakowski and others, should be placed among the Entomophthoreae, was discovered by Lohde (*l. c.*) in the prothalli of ferns and has been subsequently more thoroughly investigated by Leitgeb (*l. c.*). Its presence is indicated by brown spots upon the prothallus within the cells of which it exists in the form of short thick hyphae, which spread from cell to cell by means of slender projections. The latter penetrate the cell wall, which becomes modified around them into a sheath-like structure, and having thus gained access to an adjoining cell continue their development at its expense. The two usual forms of reproduction, by means of conidia and resting spores, are found in the genus and are of a very simple type. When about to produce conidia the short thick hyphae or *hyphal bodies*, as they may be termed for convenience, germinate sending up asexually fructifying hyphae or *conidiophores* which, after penetrating to the surface of the prothallus, become swollen at their extremities and produce ovoid conidia which are discharged into the air. After their discharge the conidia become pear-shaped, and the basal papilla of attachment to the *basidium*, or swollen extremity of the conidiophore, is protruded as a hyaline appendage (*Nabel*). The conidia germinate and spread the disease by entering other prothalli with which they may come in contact. The resting spores are formed within the cells of the prothallus, and result from the mere contraction of the contents of the hyphal bodies, which become surrounded by a thick wall. According to Leitgeb, this formation shows no indications whatever of a sexual origin, although his figures do not seem to preclude such a possibility in view of what is at present known of sexual processes in the group. The germination and further development of these resting spores have not as yet been observed. The genus is at present represented by a single species, *Completoria complens* Lohde, and has been found and cultivated by Leitgeb upon prothalli of numerous genera and species. It is at present unknown in this country. From this comparatively simple form we may now pass to the consideration of one somewhat more complicated, which is also parasitic upon another plant, in this instance a thallophyte.

The genus Conidiobolus was accidentally discovered by Brefeld in connection with his researches upon the Tremellini on which it is parasitic; and its discoverer, having obtained spores from cultures in which it had appeared, was enabled by cultivating them in nutritive solutions, to trace its development with the greatest completeness. The conidia grow readily in a decoction of horse dung, forming a mass of branched and rarely septate hyphae; which, having nearly exhausted the nutritive solution, become broken up, through the formation of partition walls, into numerous irregularly lobulated fragments which correspond to hyphal bodies, as I use the term. These lobules appear early in the development of the hyphae, in the form of irregularly swollen projections from them; and mark the points of origin, even at an early stage, whence the conidiophores are subsequently to arise. Shortly after this general disintegration of the hyphae, single, simple conidiophores arise from each fragment, in number corresponding to the swellings above described, and produce large, ovoid conidia which are discharged in the usual way. The chief interest of the genus lies, however, in the formation of its resting spores, which seem to be of sexual origin. This formation of zygospores appears as that of the conidia begins to disappear, so that both forms are at first developed side by side, while eventually the conidial formation ceases entirely,— a circumstance which seems to verify this author's previously expressed opinion that an alternation of some regularity exists between the appearance of the two types of reproduction. In the formation of these zygospores, hyphae arise from swollen projections, similar to those already described as being the origin of the conidiophores, which, after a variable develment, conjugate through the apposition of their swollen extremities, the contents of one extremity uniting with that of its fellow through the absorption of the intervening walls, and producing in one of them a thick-walled zygospore. Owing to a difference in size of these conjugating extremities, Brefeld was inclined to place the family among the Oomycetes; but the previous observations of Nowakowski[1] in *Empusa*, together with more recent studies of the family, render this improbable. In from ten days to five weeks after their formation, the resting spores were made to germinate; and sending out one or more hyphae produced usually a single conidium resembling those characteristic of the species. Of these, two are described: *Conidiobolus utriculosus* and *C. minor*, neither of which has been observed in the United States.

The genus Basidiobolus, discovered by Eidam, is perhaps the most interesting of the Entomophthoreae from the unusual differentiations which accompany its asexual as well as sexual reproduction. Unlike other members of the group the species are wholly saprophytic, occurring naturally upon the dung of frogs and lizards after evacuation; while they may be readily cultivated in nutrient solutions similar to those employed by Brefeld in his study of *Conidiobolus*. According to Eidam, the fungus is present in the digestive tract, only in the form of spores or hyphal bodies which are dormant until they are evacuated with the faeces upon which they subsequently develop, forming large colorless hyphae with numerous cross partitions. These hyphae do not become broken up into hyphal bodies before reproduction commences, except in so far as this condition may be approached in cases similar to that figured by Eidam[2] where, in a concentrated nutrient solution, the segments of the hyphae become rounded; but do not, however, break apart as in *Conidiobolus*. In reproduction the hyphal segments may produce slender single conidiophores which, rising vertically, become greatly swollen at their extremities. From the apex of this conidiophore the large conidium buds and, during its formation, the swollen extremity which bears it becomes modified by the contraction and thickening of its walls into a peculiar piece or *basidium*, which is discharged, together with the conidium, by the explosion of the slender conidiophore.

[1] *l. c.*, A. [2] *l. c.*, Pl. IX, fig. 10.

The formation of zygospores is also quite peculiar, and always results from the conjugation of two adjacent cells in *the same* hypha, except in some instances where two conidia may conjugate directly. In either case conjugation is preceded by the formation of finger-like processes from either of the conjugating cells, which, arising opposite each other, are usually closely applied. Conjugation, however, does not take place by means of these processes which, at first sight, would suggest a *Rhynchonema*-like type; but by the absorption of the partition wall between the conjugating cells and the direct passage of the contents of one into the other. In this instance, as well as in *Conidiobolus*, the cell in which the zygospore is to be formed is recognizable before conjugation by its larger size. The function of the finger-like processes above mentioned seems wholly connected with the division of the nuclei which pass into them and become divided in two parts; the upper portion disappearing without becoming a new nucleus while the lower passes as a nucleus into the zygospore. The zygospores are of two varieties: one, larger than the more common form, is very thick walled and covered by a peculiar brown incrustation which renders it opaque; the smaller and more usual variety was made to germinate in nutrient solutions and produced hyphae which developed the characteristic conidia of the species.

Two genera remain to be mentioned: *Tarichium* of Cohn and *Massospora* Peck. The former, as has been several times pointed out by writers on Entomophthoreae, is, without doubt, merely the resting stage of some *Empusa*, the conidia of which are as yet unknown. In *Massospora*, however, which has not, I believe, been previously referred to the present family, we have a form quite peculiar, the near affinities of which cannot be determined by reason of the absence of any knowledge concerning the formation of its resting spores, or the germination of the multitudinous internal spores which characterize the genus.

With this brief mention of the remaining genera we may now pass to a consideration of the genus *Empusa*, which, with its subdivisions, includes only entomogenous forms. I have preferred to consider these subdivisions as a whole under *Empusa* as a matter of convenience, as well as from the fact that I am not at present inclined to believe that they have more than a subgeneric value; but my reasons for this course, as well as for my use of the name *Empusa* in preference to *Entomophthora*, may be better given hereafter when the principal morphological differences in the species have been touched upon.

The Genus Empusa.

Infection and production of hyphal bodies.—As has already been mentioned, infection among entomogenous Entomophthoreae results from contact with a conidial spore which, adhering to the insect host, enters its body by means of a hypha of germination. The exact method of this entrance is hardly a subject for actual observation unless, perhaps, in insects which, like many aphides, are semitransparent, and, owing to their soft integument, afford an easy entrance to the hypha at almost any portion of the body. In other insects, more especially beetles, grasshoppers, ichneumons and the like, the horny integument must diminish considerably the chances of infection; and in such cases the stigmata or the thin membrane connecting the body segments and leg joints must be the principal points of entrance. Infection, resulting from the ingestion of spores with the food, does not, I think, occur as is indicated by experiments with wood crickets which will be mentioned under *E. Grylli;* and, as a rule, the digestive tract during life does not seem to be penetrated by the fungus.

After the hypha of germination has entered the body of the host, it develops with some rapidity at the expense of the softer tissues. This growth usually differs from that described in *Conidiobolus* from the fact that, instead of producing a branched mycelium, the hyphae multiply, not by branching and continuous growth, but by the formation of what I have previously called hyphal bodies, which consist of short, thick fragments, of very varied size and shape, that are continually reproduced by budding or division until the insect is more or less completely filled with them. In some instances these hyphal bodies have been observed as naked masses of protoplasm with an amoeboid movement, as is stated to be the case in *E. colorata;* but in most instances a cell wall may be demonstrated. In *E. Grylli*, at an early stage, the hyphal bodies may be seen loosely adhering in clusters as a result of continued budding; but more often in this and other species they occur singly or in pairs. It is probable, however, that this mode of development is subject to considerable variation and that in some instances a mycelium may be produced directly, after the entrance of the germinating hypha. I have been unsuccessful in endeavoring to cultivate conidia in sterilized solutions; although, by employing a drop of water in which numerous aphides had been crushed, I was enabled to obtain a fairly vigorous growth from the conidia of *E. aphidis*. In this case the germinating hypha branched in all directions, forming a considerable mycelium with numerous septa; but, owing to the lack of nutriment as well as to the presence of bacteria, the hyphae soon became much attenuated and finally died. DeBary[1] states that this production of a mycelium as a first result of infection occurs in *E. ovispora*, *E. curvispora* and *E. sphaerosperma* (*radicans*); but, according to Nowakowski, in his summary of the Empusae, the first two are not thus characterized, while my own observations of *E. sphaerosperma* do not bear out his statement that the "fungus growth" within the host is filamentous in all cases. It seems not improbable that both forms of development may occur under different conditions; but, however this may be, the termination of the first or merely vegetative condition of the fungus consists in the production of a mass of hyphal bodies which fill the host more or less completely; and in no instance, I believe, is this stage or its equivalent omitted by the direct growth of the original hyphae into conidiophores. On this assumption, in cases where a direct mycelial growth follows the entrance of the hypha of germination, if indeed such instances occur, this mycelium must fall to pieces into hyphal bodies, before the commencement of growth the direct object of which is reproduction, in a fashion resembling that above described at a similar stage in *Conidiobolus*.

The hyphal bodies, the production of which usually marks the end of any appropriation of nourishment from the host and generally occurs at about the time when the host has ceased to live, are in many cases somewhat different from those which have previously characterized the fungus and often possess great regularity, both in size and shape, closely resembling spores. In *E. Fresenii*, for example, the original hyphal bodies

[1] Vergl. Morphol. d. Pilze, etc. [2] *l. c.*, B, p. 176.

are such as are represented in figs. 106–108, while fig. 127 shows examples of those which precede the spore formation and are derived from them. In other cases, the ultimate hyphal bodies may be very irregular in size and shape. In all instances, they contain a highly concentrated fatty protoplasm and are capable of subsequent and often very extended development.

Having reached this condition by the production of a mass of hyphal bodies, the fungus, under favorable conditions of temperature and moisture, may proceed at once to the completion of its development; but if these conditions are absent, a resting or chlamydosporic condition supervenes, in which the contents of each hyphal body become surrounded by a single wall of variable thickness according to the duration of this enforced resting stage. In this manner, the fungus may remain dormant for a considerable period until the presentation of proper conditions for further growth. How long the chlamydospores may live, I am unable to say; but I have observed their germination after several weeks, and they probably retain their vitality for a much longer period, and may perhaps hibernate under certain circumstances. They form a very convenient means for the cultivation of Empusae in water, in which they proceed at once to the formation of conidia or of resting spores. The period from first infection to the formation of chlamydospores or hyphal bodies, prior to the commencement of the reproductive growth, varies according to the host. In very minute and ephemeral insects, such as many gnats that are commonly attacked, the period must necessarily be short, not exceeding two or three days; but in cases where I have been enabled to observe this period, which has been unfortunately only in connection with the larger hosts, such as flies and caterpillars, it varies from six to twelve days.

Germination of the hyphal bodies and chlamydospores.—Having appropriated the whole or the greater portion of the nourishment afforded by the host, the fungus is now ready to expend it in the second or reproductive stage of its growth. Under the influence of a moist atmosphere and a sufficiently high temperature, the hyphal bodies "germinate" with great rapidity. The amount of moisture needed to produce this germination is variable in different forms. In the common house-fly fungus (*E. muscae*), for instance, a slight change in the amount of atmospheric moisture is sufficient to produce conidial formation and discharge. This is very noticeable on the seashore, where slight changes of the wind on or off the water produce a very rapid and noticeable effect upon flies thus parasitized when observed in the ordinary atmosphere of the house. In other instances, more especially in those species which, unlike the house-fly fungus, are characterized in their conidial reproduction by a considerable external growth of hyphae, a much greater degree of moisture is a necessity. Extreme cases of this kind are found in species such as *E. conica* or *E. sepulchralis* which occur only in very moist situations.

In germinating, each hyphal body or chlamydospore sends out one or more hyphae which grow with great rapidity; but the manner of this germination, together with the subsequent development of the resulting hyphae, varies considerably in different species and under different condition. In the simplest case a single hypha thus produced may grow directly to the outer air and then produce a single conidium or set of conidia, according to the type peculiar to its conidiophores. In other cases, a single primary hypha may branch indefinitely, each ultimate branch becoming a conidiophore similar to those of the more simple case just mentioned. This usually occurs where the conditions of growth have been very favorable and may be found side by side with the more simple form.

Although the number of germinating hyphae developed from a single hyphal body is usually small, not as a rule exceeding one or two, certain instances occur in which the number is considerable. In *E. conglomerata*, for example, as described by Sorokin, long hyphal bodies are found which germinate in all directions and are not unlike, in this respect, the hyphal bodies previously mentioned in *Conidiobolus.* These hyphae subsequently branch and anastomose, forming a coherent mass which Sorokin has termed a *stroma*, and on which he has based a classification of *Empusae* into "Stromaticae" and "Astromaticae." It is probable, however, that this condition is interchangeable with the more ordinary form, since in some specimens for instance of *E. apiculatus*, I have found well marked stromata, while in others the direct development of the conidiophores from hyphal bodies has been distinctly traceable.

The most singular modification of this kind, however, occurs in *E. aphidis* and *virescens* which are the only species thus far in which it has come under my observation. Here we have a body which appears to be of the same nature as the hyphal bodies in other species, of regular spherical form and with a highly refractive fatty contents, from which, soon after the death of the host, hyphae begin to germinate in all directions and in incredible numbers, in a fashion that reminds one of a head of *Aspergillus* (figs. 239 and 261). The hyphae thus produced then branch and divide, becoming separated into a mass of irregular, short, contorted hyphae which fill the host and distend its body. This breaking to pieces of hyphae produced from hyphal bodies also is found in species where the usual type of germination occurs: as in *E. muscae*, in which, just before the emergence of the conidiophores, the body cavity contains a mass of irregular short hyphae together with germinating hyphal bodies.

Formation of conidiophores.—The germination of the hyphal bodies results either in the production of sexual or asexual resting spores (zygo- or azygospores); or of conidiophores bearing *conidia.* In the latter instance hyphae, arising directly or indirectly from the hyphal bodies, grow rapidly outwards, burst through the less resistent portions of the host's integument in spongy masses, in most instances of a livid white color. These masses sometimes vary to pale or bright green or dull olive, even in forms where their normal color is white; and there is considerable variation in their general appearance according to the species or to the conditions of their development. In some cases, they barely project beyond the body of the host and are confined to the points of emergence which are generally afforded by the thin intersegmental membranes through which they project in cushion-like rings as in *E. muscae.* In other cases, the external growth may be more extended and the masses may coalesce so as to cover the whole body with a continuous layer of conidiophores which may form a mass several times as large as the insect from which it springs.

In the first and more simple case, where there is little external fungus growth, the cushion-like masses are usually formed by *simple* conidiophores (fig. 1) which, although each may be derived in common with many others from the same hyphal body, are yet ultimately simple, producing few or no branches outside the host's body and giving rise to a single conidium. In the second instance, where the external growth is greater, a different type usually occurs in the conidiophores. Not only is the external branching very considerable, but the ultimate divisions of each conidiophore are arranged in a corymbose or digitate fashion, as in figs. 202 and 220. This occurrence of simple and compound conidiophores in different species has led to the generic separation of the two groups; yet the distinction is by no means absolute, and intermediate forms occur, as in *E. culicis*, *E. apiculatus* and a few additional species. The converse is also true, and simple conidiophores are very commonly found in species where the type is usually compound. As has been already remarked, the growth of conidiophores is very rapid under favorable conditions; and an insect containing hyphal bodies, if placed in a damp, warm atmosphere, may give rise to the characteristic white masses in a few hours. Soon after the appearance of these masses the production of conidia commences, and this brings us to the next step in the conidial development.

Formation and discharge of the conidia.—The terminal portion of the conidiophore, whether this be simple or one of several digitations, is termed the *basidium* and is usually swollen to a greater or less extent. From the apex of this basidium, which is homologous with similar structures occurring among the Mucorini, the conidium, or more properly the mother cell of the conidium, is formed by budding. This bud increases at the expense of a portion of the contents of the basidium, until it has attained very nearly the normal shape and dimensions of the conidium; when it becomes separated from the basidium by a cross partition, which forms at first a horizontal plane of separation between the two and is homologous with the *columella* of the Mucors. Within the mother cell thus formed is developed a single conidial spore, the walls of which are normally in close apposition to those of its containing cell, which must thus be considered a sporangium reduced to its simplest terms and modified to combine economy of material with a judicious dissemination. The resemblance to a one-spored sporangium is clearly seen in cases where, through the absorption of water by osmosis, the wall of the mother cell becomes separated from that of the conidium; a phenomenon which is very commonly seen after, or even before, the discharge of the conidium, and is sometimes carried to such an extent that the conidium may be seen floating free in a large spherical mother cell (fig. 321).

When the conidium is fully developed, and even previous to this, the contents of the spore, as well as of the basidium, begin to expand through the absorption of water. At first, as a rule, the contents of the basidium exert the greater of the two forces thus produced; perhaps owing to the fact that a more rapid absorption of water is possible through its single wall than through the double wall of the conidium. For this reason, the columella is at first forced outwards into the conidium towards which its convexity is thus turned. In some instances, especially in cases where the basidia are large and strong, this condition of things may continue until the discharge of the conidium. Such is apparently the explanation of the appearance figured by Nowakowski[1] which is referred to by Eidam[2] as a mechanism for discharge, very different from that usually found in Empusae. I think, however, that this will prove to be only an extreme case of the nature just described. In my own experience I have observed this appearance only

[1] *l. c.* B, Pl. xi, fig. 82, etc. [2] *l. c.*, p. 186.

infrequently in the species referred to, *E. Grylli*, and in allied forms (fig. 83). It should be noted that contraction of the spore contents from any cause might also produce the same condition. In by far the majority of cases, the contents of the conidium, being more dense than that of the basidium, finally exert a greater pressure and forces the columella back into the basidium, thus reversing its former position. The sum of these opposing forces is very considerable, and as a natural result of their action a rupture of the wall ensues at the point where they are opposed, that is, in a circle round the base of the mother cell. This circle of rupture is usually very evident in discharged conidia, being indicated by a slightly ragged projection which forms a ring at the base of the papilla (fig. 85). As a result of this rupture, the conidium is discharged violently into the air, often to a considerable distance. The columella commonly remains unbroken by this discharge, although it is often greatly stretched and hangs from the basidium as a tongue-like projection. In other instances it may be accidentally broken or this rupture may be normally connected with the discharge. In the latter case, a portion of the protoplasm from the basidium is discharged with the spore and serves to fix it to any object with which it may come in contact.

The presence or absence of a columella in different species has been made a point of structural difference to which more weight has, I think, been given than is justified by the facts. The assumption that a columella exists and is wholly or partially destroyed by the discharge of protoplasm above alluded to, in cases like *E. muscae* for example, seems to me at least as warrantable as the apparently needless assumption of the absence of so characteristic a structure. Moreover, the presence of a ruptured columella is often indicated even in *E. muscae* by the numerous shreds that may be seen adhering to the basidium after discharge (fig. 2).

The conidia and their germination.—The conidia in their normal condition are of various size and form, often varying considerably in the same species. The extremes of shape are well represented by the nearly spherical spores of *E. muscae* and the slender tapering form of *E. gracilis*. In size they vary from about 10μ in length to 75μ or over. They are usually hyaline, rarely slightly colored, with a fine granular contents; or, more commonly, contain coarsely granular protoplasm with large fat globules. In many instances, these fatty bodies are so regular in size and shape that the conidia resemble asci filled with spores; a fact which probably accounts for the statement "Flocci fertiles intus sporidiis globosis referti" in a description of what seems undoubtedly an *Empusa*, by Fries.[1] The common occurrence, also, of very large single oil globules seems to have caused a similar error. The walls of the conidium are, so far as known, always smooth, without spines or similar modifications, and possess an adhesive quality which serves to attach them readily to any object, even when their discharge is unaccompanied by the mass of protoplasm above described. The basal portion of the spore is always more or less papillate, the papilla being in reality that portion of the spore proper which projects from within the mother cell, from which it is distinguished by the ring of dehiscence.

The conidium when discharged, if by chance it has come in contact with a suitable host, adheres to it, and sends out a hypha of germination which enters its body as previously described. When placed in water the conidia give rise to one or more hyphae

[1] *l. c.*

which branch and elongate, growing constantly more attenuated, their protoplasmic contents becoming separated by successive cross partitions from the empty hyphae left behind (fig. 240). It may here be mentioned that this separation by cross partitions is common in the general growth of the fungus. The hyphae produced thus from conidia have the usual characteristics: a granular protoplasmic contents which often shows a very noticeable streaming motion, and contains large oil globules and a hyaline wall. The power of germination lasts, according to Brefeld, at most only a week, or slightly more in *E. radicans* (*E. sphaerosperma*); but in my own experience I have found the period usually much shorter than this. The period is in all probability very variable; spores that have been formed under unfavorable conditions being better able to withstand similar conditions: the endurance of the spores, moreover, varies with different species. As a rule, germination takes place very soon after discharge, and if the conidium has neither fallen upon a proper host nor upon a wet surface it proceeds to form

Secondary conidia.—The secondary conidium is a provision for further dissemination in case the primary spore has fallen on a substance unsuited to its proper development. The most common method of formation consists in the production of a hypha of variable length, which, growing vertically upwards, becomes swollen at its extremity into a basidium, and produces a conidium similar to that whence it is derived. This is discharged in the usual fashion, and may in turn produce tertiary, etc., conidia, in a similar way, until its vitality is exhausted or it has found a suitable lodgment. The conidiophore formed in this process is usually simple, even if the type from which it was derived is digitate; yet I have seen, in a case where numerous spores had been discharged upon wet moss, that the hyphae arising from them united to form a mass of conidiophores of the digitate type peculiar to the species.

Although the form of secondary conidium just described is most commonly found, and is apparently the normal type in all species under favorable conditions, it is subject to several interesting variations that are dependent, for the most part, upon an insufficient supply of moisture. The first of these consists in the production of a secondary conidium quite different from the primary, either by direct budding from it (fig. 9), or borne upon a short hypha of germination (fig. 362). These conidia are also discharged; but are apparently better suited to resist unfavorable conditions than the ordinary ones, and probably retain their power of germination much longer. The most singular modification, however, is presented by a few species allied to *E. sphaerosperma* and *E. Fresenii*. In these forms and their allies, when the conditions of moisture are unfavorable for the ordinary process, a long, slender, capillary conidiophore is produced, on the end of which is borne a peculiar secondary conidium differing still more widely from the parent spore than in the case just mentioned.

These secondary conidia (figs. 157, 191, etc.) are, with one exception, nearly almond-shaped, with noticeably thick walls, and are not discharged. Whether they ever produce tertiary spores similar to the primary ones, I have been unable to determine; but the formation from them of tertiary conidia similar to themselves is not uncommon. They may often be seen germinating by means of an irregular hypha which, beginning as a drop-like protuberance from the apex of the spore (fig. 119), may grow to a considerable length (fig. 122). Eidam, in his paper on *Basidiobolus* (Pl. 9, fig. 16), figures a mode of germination in this genus of a related type; but as the author describes the swollen extremity of the conidiophore as a *basidium*, the similarity is not so striking as a comparison of this with fig. 119, for example, in the present paper, would lead one to infer.

Cystidia and rhizoids.—Before leaving the conidia and conidiophores, two additional structures must be mentioned, which are of some importance morphologically. These are the so-called *cystidia*, or paraphyses as they have been called; and a modification of certain hyphae, known as *rhizoids*, which serve to attach the host to the substratum on which it rests. The cystidia are usually simple hyphae, exceeding the conidiophores in size, and projecting beyond them, often to a considerable distance. In some instances they are very large (fig. 306), and readily seen with the naked eye; while in others they do not differ from the conidiophores. They are not, I think, homologues of paraphyses in other fungi, and their office is unknown; unless, perhaps, they may be considered as rhizoids which are functionless from their position; an explanation which seems to me very probable. A modification of the paraphyses should be mentioned which occurs in *E. echinospora*, a species in which, contrary to the usual type, the zygospores are very commonly produced externally. In this case, when the sporophores have emerged from the host, certain of their number may be seen projecting beyond the rest (fig. 297). While the process of spore formation is going on, these hyphae grow rapidly, forming ultimately a delicate network about the mass of mature zygospores.

The hyphae of attachment, or rhizoids as they may be conveniently termed, consist of hyphae which, growing from the lower and outer portions of the fungus mass, attach themselves to the substratum upon which the host rests and serve to hold it firmly in position. The rhizoids may be simple or variously branched, and their termination may be variously modified into an expanded "sucker" (fig. 249). They do not, I think, enter into soft substances, and their adhesion is apparently due to the presence of a viscous secretion. They are produced with great rapidity, appearing even before the host is dead, and increasing in number with the appearance of the conidiophores. Rhizoids are confined to certain species, and generally accompany the digitate type of conidiophores; their presence should not, however, in my opinion, be considered of any importance as a generic distinction.

It is now necessary to return once more to the condition in which we find the host filled with chlamydospores, or hyphal bodies, in order to examine the phenomena connected with the

Formation of zygospores and azygospores.—As has been previously remarked, the germination of the hyphal bodies or chlamydospores may result in the production of conidia above described; or may lead to the formation of spores called *resting spores*, of a very different nature, and adapted to withstand successfully conditions that would prove fatal to the conidia in a short time. The passage to this resting condition may be accomplished by a wholly non-sexual process, in which case the resulting spore has been termed an *azygospore*, or by sexual union of a type similar to that found in the Mucorini. The spores thus formed are usually of large size, spherical with one exception; with a highly refractive fatty contents; surrounded by triple walls, the outer thin and representing the wall of the mother cell, the second much thicker, and the inmost usually as thick as or thicker than the other two combined.

The simplest process by which azygospores are formed is presented by the case in which the contents of a hyphal body become directly converted into a resting spore, usually contracting somewhat and surrounding itself with two walls, the normal third wall being represented by that of the hyphal body, within which the spore may be entirely free, or to which it may be closely applied. A modification of this process occurs sometimes in the case of chlamydospores, which may be transformed directly into azygospores by the deposition of a third inner wall.

Azygospores may also be formed in a variety of ways from hyphae of germination arising from chlamydospores or hyphal bodies, or not uncommonly by direct lateral budding from them. In the first case the azygospore may be terminal (fig. 40), at the apex of a hypha of greater or less length, or may bud laterally. This process, which may be readily seen by cultivating chlamydospores in water, resembles at first the analogous formation of conidia; the end of the hypha, however, does not produce a bud, but becomes swollen into a mother cell, which is not separated from the hypha by a cross partition, and within which the double-walled spore is formed. Still another method consists in the production of azygospores interstitially (fig. 81), which is common in certain species and leads to the occurrence of spores having very irregular shapes.

These in general are the more common types of azygosporic formation, of which there are numerous slight modifications. Where true zygospores are formed, a considerable amount of variation is exhibited in the process as it occurs in different species; and although the sexual nature of the spore is beyond question in some instances, it is not so well marked in others, and may, as Nowakowski has suggested, represent a transitional form from the truly sexual to the wholly asexual processes. Such instances are found in *E. sphaerosperma*, a species in which, according to Brefeld, the production of resting spores follows the septation and anastomosis of a mass of hyphae filling the host, the spores being produced laterally from these hyphae without regard to the points of anastomosis. In my own experience I have observed something of this sort in the legs of insects attacked by *E. sphaerosperma* and its near ally *E. occidentalis;* but in the bodies of the hosts examined, which, it should be remarked, were of a very different nature from those (*Pieris* larvae) studied by Brefeld, I found only short, contorted hyphae producing spores apparently in a wholly asexual manner (fig. 217), but associated with them, numerous instances where the budding spore was directly associated with a cross-partition or a slight lip-like fold indicating the previous existence of such a partition (figs. 214–216). Whether spores thus formed should be called zygospores seems at least doubtful, and the partitions described may indicate merely the ordinary division of the hyphae. In a very few cases, however, I have, in these two species, seen a process as well marked as that represented in fig. 197, occurring in the legs of certain hosts where, as a rule, the hyphae attain a considerable length. This certainly looks like true conjugation, and may lead us to cases where the presence of a sexual union is hardly to be questioned. The first instance of the latter class discovered among the Entomophthoreae is that described by Nowakowski[1] in his three new species, *E. conica*, *E. ovispora* and *E. curvispora*. In this type we have hyphae, within or without the body of the host, producing lateral outgrowths at opposite points of two different hyphae, which meet

[1] *l. c.*, **A.**

midway between the two conjugating cells in a fashion analogous to the similar process in *Spirogyra*. The intervening walls between these two gametes, or conjugating outgrowths, are then absorbed and a mingling of their contents ensues. A bud then appears (fig. 322) on one or both the gametes, which increases rapidly, as a rule appropriating the entire contents of each conjugating cell to form the zygospore. A septation of the hyphae above and below the point of conjugation is often seen, but is not invariable, resembling in this respect the similar process in *Conidiobolus* previously described. It may be mentioned, in passing, that the chief distinction between the two rests on the fact that here we have a zygospore formed by budding, while in *Conidiobolus* the spore is produced directly within one of the conjugating cells. In this, as in other cases, the empty hyphae disappear rapidly after the zygospores have been formed; a circumstance which, together with the rapidity of the process as a whole, accounts for the infrequency with which conjugation in *Empusae* can be observed. In one case, however (*E. rhizospora*), the hyphae after conjugation become brown and horny, holding the spores firmly in a spongy mass (fig. 374); but even here the process of conjugation can only be seen during a short period, while the spore is developing, owing to the subsequent contraction and distortion of the hyphae.

In *E. echinospora*, in which the zygospores are often external, a modification of this *Spirogyra*-like process is found, which deserves to be mentioned. Here (figs. 298–302), we have a conjugation taking place between two filaments in a manner similar to that described above; but, instead of arising by budding from one of the gametes or in their immediate vicinity, the spore commonly develops as a terminal swelling from the end of one of the conjugating hyphae.

In addition to these types of conjugation, a singular form, not, I believe, noticed hitherto in Entomophthoreae, occurs in *E. Fresenii*. It is, as far as I have observed, invariable in this species and is never associated, as is usually the case, with the production of azygospores. The hyphal bodies, as they occur in the host just prior to the production of conidia or zygospores, are almost perfectly spherical and very uniform; and are derived from large, shapeless bodies which have the appearance of naked protoplasm. The spherical hyphal bodies lying side by side within the host proceed to conjugate in a manner indicated in the succession of figures 127 to 135. A slight projection first appears from the upper inner end of either hyphal body (fig. 128). These projections soon meet midway between the hyphal bodies (fig. 129), after which a bud begins to rise directly above their point of union (fig. 130). The contents of both bodies pass into this bud, forming the mother cell of an elliptical zygospore which, I believe, affords the only known exception to the usual spherical shape. After the spore is mature, the two hyphal bodies usually persist for some time as bladder-like appendages (figs. 135–136), which slowly disappear (figs. 137–140).

This is certainly a very simple process, yet it demonstrates I think, more clearly than has yet been possible among Entomophthoreae the existence of an undoubtedly sexual process of a distinctly zygosporic type. In *Conidiobolus*, *Basidiobolus*, and even in the examples from *Empusa* previously given, there is usually a more or less marked difference in the size of the gametes, which, in the first-named genus, led Brefeld to consider the family as belonging to the Oosporeae; but, in the present instance, we have the gametes exactly alike, and in addition to this a process of development in the zygospore similar to that occurring among the Mucorini in *Piptocephalis*. The regularity of this process, and of the resulting zygospores, is worthy of mention; and although the hyphal bodies are collected in an indiscriminate mass, the details of the process never show the slightest variation from that described above.

Before leaving the subject of conjugation in Empusae, a singular method, by which the resting spores of *E. Grylli* are often formed, must be described. This species is remarkable for the great variety it exhibits in the details of the formation of its azygospores; but in certain cases it seems not impossible that even in this species we may have true conjugation of a type quite different from those previously described. The successive figures, 31 to 35, indicate the nature of this process. In the first place we have, before reproduction of either type, a condition characterized by the presence of irregular, rounded hyphal bodies of various size and shape (fig. 31). Instead of producing an azygospore by any of the methods above described, one of these bodies may become septate by the formation of a median cross partition (fig. 32). An elevation of the cell wall presently appears around the hyphal body, between the cells thus formed, which develops into a two-lipped fold (figs. 33 and 34). The partition between these two cells is then apparently absorbed, for the contents of one gradually pass into the other to form a "zygospore" (fig. 35). A variation of this process is found in the similar division of the swollen extremity of a hypha (figs. 38–39) the lip-like folds in each being quite peculiar. In many cases the formation of a resting spore is not accomplished by a single division and subsequent union; but only results after a succession of oblique divisions always accompanied by the lip-like folds, as in figs. 36 and 37. Spores of this kind are usually characterized by their flattened bases, and in some instances two such spores may be formed, one in either cell of the divided hyphal body, as often occurs in other conjugating cells. Whether this is in reality a form of conjugation, I do not feel prepared to say; and careful observations, by means of cultivations of the hyphal bodies, are much to be desired. This process may in a measure explain the appearance previously alluded to (p. 147) and represented in figs. 214–216. Here there is no production of a lip-like fold, yet it seems not impossible that in such cases a short hypha may have divided and conjugated with itself, so to speak; the zygospore arising as a lateral bud instead of developing directly within one of the divisions. Such an explanation may seem somewhat far-fetched, yet the division of a hypha and subsequent conjugation with itself are practically what occurs even in *Basidiobolus*.

The mature azygospores as well as the zygospores in all known species are, with the exception of *E. Fresenii*, spherical in shape; and in the majority of cases are indistinguishable in the different species, except by slight variations of size. There are, however, three notable exceptions to this rule. The spores of *Tarichium megaspermum* Cohn[1] are characterized by a deep brown outer wall, or *epispore*, which is marked by sinuous reticulations. In *E. echinospora* (figs. 303–305), the epispore develops numerous sharp spines which separate it from all other known species; while in *E. rhizospora* the brownish spore is held by numerous rhizoid-like outgrowths from its base (figs. 374–375). A dark brown epispore seems also characteristic of *E. calliphorae* Giard (*E. muscivora* Schroeter).

[1] *l. c.* B.

In my own experience, I have never observed the germination of resting spores in any instance, although I have continued cultivations of them in water for upwards of three months. I have not, however, had an opportunity of adopting the plan suggested by Eidam of cultivating them in nutritive solutions, and a trial of this method might lead to more satisfactory results. A germination of the resting spores of certain species is reported by Nowakowski, Sorokin and Krasilstchik; and the first-named author states that such spores placed in water in the autumn germinate during the following spring. I have, however, seen no account of successful cultures of this nature unless it exists in the text of Nowakowski. The description given by Krasilstchik of a species (*E. uvella*), in which he obtained a germination in *four days*, seems hardly reconcilable with the facts as known in other genera. From analogy with *Basidiobolus* and *Conidiobolus*, it is not to be questioned that the resting spores germinate, as in these cases, producing the usual conidia; but whether this has been determined by actual experiment, I am unable to say. The period of rest before germination is probably very variable, and its primary object is, of course, to afford a means of hibernation, or of withstanding similar protracted conditions unfavorable to development, and of long duration. Although a single season is probably the normal period of this resting state, it has been suggested by Brefeld that it may be extended over more than one season, thus allowing the insect host to recover from the effects of *Empusa* epidemics.

The causes which induce the formation of resting spores can be explained with as little satisfaction among Empusae as in other similar cases. The observations of Brefeld in his experiments with *E. sphaerosperma* Fres. (*E. radicans* Bref.), which indicated that their production takes place towards the end of the season, gradually supplanting the conidial form, are not corroborated by my own experience. This, at least, does not seem to be the course followed in the natural development of the fungus out-of-doors; since the examination of some thousand or more of specimens shows that as a rule the relative number of individuals of a given species, which contain resting spores, remains about the same from the middle of June to the middle of October. Whether the production of resting spores bears any relation to the number of previous generations of conidia is a matter to be determined only by careful and repeated cultures in different cases. None of the remaining causes usually assigned as inducing zygosporic formation have any apparent influence in the present instance. But here also repeated experiments in different cases, under known and variable conditions of moisture, temperature and nutrition, are necessary to determine whether variation in these respects seems to have any definite connection with the kind of spores produced.

The hosts of Empusae include representatives from all the hexapod orders; but among them the Diptera are the greatest sufferers, at least in so far as the number of Empusae which prey upon them is concerned. The Hemiptera come next, followed by the Lepidoptera and Coleoptera; while the Neuroptera, Hymenoptera and Orthoptera are about equally affected, and are attacked by two or three species, only, in each instance. The liability to infection is shared by both larvae and pupae as well as by imagines, although the latter are most commonly affected. In insects where the larvae and pupae differ but slightly from the imago, both these stages are equally susceptible to the disease. Mr. L. O. Howard has also shown me specimens of *E. Grylli* that had developed upon the common web worm (*Hyphantria textor*) *after* pupation; but this occurrence is certainly unusual. Among Lepidoptera, I have been surprised to find the imagines attacked in numerous instances, a fact, I believe, not hitherto observed; and one species (*E. geometralis*) seems peculiar to them. Geometridae, Noctuidae and Tineidae may be affected, and I have even found the common sulphur butterfly (*Colias philodice*) thus attacked. The species or family of the host has hitherto been generally considered a means of determining the species of *Empusa*, in most cases, with some accuracy; yet my observations have shown that this is by no means the case and that specific distinctions, based largely upon the character of the host, are of little value. The variety of hosts attacked by a single species is sometimes very great, perhaps in no instance more so than in *E. sphaerosperma.* I have specimens of this form upon the larva of *Pieris*, on the imago of *Colias philodice,* Diptera of several families and genera, *Phytonomus* larvae (Coleoptera), the common rose-leaf hopper (*Typhlocyba*) and *Aphis* (Hemiptera), on ichneumons of several genera and a small bee (Hymenoptera), and on a species of *Thrips* (Thripidae), while in Europe it is also recorded on *Limnophilus* (Neuroptera). With such a diversity possible in the hosts, it is obviously unsafe to describe, as new species, forms without peculiar characters of their own, merely because they occur in a new host, or to give any considerable specific weight to the character of the host in support of slight variations in the shape of the conidia or the size of the resting spores.

In certain instances, where several Empusae were found together, I have noticed two species developed upon a single host; for example, *E. Aphidis* and *E. Fresenii*, as well as *E. conica* and *E. papillata; E. gracilis* and *E. variabilis; E. lageniformis* and *E. occidentalis.* It is, therefore, not always safe, where such proximity exists, to refer the resting spores that may occur in connection with conidia to the same species of *Empusa.*

The habitat of Empusae is various, one of the most productive localities being the margins of brooks in shady woods. Certain species are found only in such situations, adhering to wet substances, such as moss, logs, stones, etc., in the water or along its margin; a constant supply of moisture being apparently necessary for their development. In other cases dryer situations are preferred, and the fungus readily withstands the alternate dryness and moisture consequent upon the variations of weather, producing its conidia repeatedly, whenever the atmosphere is sufficiently moist, until the conidiophores are exhausted. Many hosts, before death, seek conspicuous positions by crawling upwards on grass, or other substances, whence the conidia are discharged over a considerable area. Perhaps the favorite position assumed by hosts before death is upon the under side of leaves in shady situations in woods or about houses, where a careful search during wet weather seldom fails to disclose numerous specimens. I have noticed only one species which occurs on flowers attractive to insects, namely *E. Muscae;* which, although common in all parts of houses, I have only seen in nature on the flowers of *Solidago* and contain certain Umbelliferae.

Miscellaneous notes.—In collecting Empusae I have found that, as a rule, foggy weather is the most favorable for the purpose, since they are more conspicuous when distended by moisture. A shallow tin box, partly filled with moist *Sphagnum*, is a convenient receptacle for specimens; and the latter should be kept separate. In the laboratory each specimen should be inverted over a slide or cover in a moist chamber, until a sufficient number of conidia have been discharged, when it may be dried for the herbarium. Conidia, obtained in this way, may usually be kept for reference for an indefinite period; and, since they allow the comparison of very large numbers of spores side by side, are most convenient for study.

The artificial propagation of Empusae, by the infection of fresh hosts, I have found a much more difficult matter than one would suppose, even when the host infected was of the same species as that from which the spores were obtained for this purpose. Infection between dissimilar hosts I have found still more difficult; although, in two instances, I have been successful in infecting caterpillars with *E. Grylli* developed on grasshoppers, as well as in transferring *E. sphaerosperma* from leaf hoppers (*Typhlocyba*) to a *Pieris* larva. The method which I have adopted for infection consists in the use of a tightly-covered jelly tumbler in which the upper portion is separated from the lower by a round piece of wire netting. By placing the hosts to be infected in the lower of the two chambers thus formed and fastening a specimen of *Empusa* in the upper one, the living hosts below can hardly escape the spores discharged through the netting.

The period which ensues after the infection of a host until its death varies to some extent. In the larger hosts, such as flies or caterpillars, death may not take place for twelve days; although the usual period is from five to eight days. In minute hosts this period must be considerably shortened, owing to the ephemeral character of many forms known to be subject to the attack of Empusae. The first visible symptom of the disease is a general restlessness of the host. In caterpillars, for instance, the insect leaves its food plant and wanders restlessly about; usually endeavoring to climb upwards before death, which is apparently quite sudden and unaccompanied by contortions of the body. The host insect thus remains clinging to the object on which it rests or is fastened to it by rhizoids. Certain insects are fixed by the insertion of their probosces into the substratum on which they rest, as is the case with aphides. The house-fly is, I believe, always fastened by its proboscis which adheres firmly to the substratum. Where rhizoids are developed, they often appear before the death of the host, and I have seen a geometrid moth, which was thus firmly attached to a pine needle, fluttering violently in its attempts to escape.

In the account of the separate species of Empusae which follows I have used this generic name for all the forms, employing the names *Entomophthora* and *Triplosporium* in brackets as groups of subgeneric value. In *Empusa proper* I have included forms in which the branching of the conidiophores is of the simple type, and the formation of resting spores presumably asexual, taking *E. Muscae* as the type. Under *Triplosporium*, I have included the two forms *E. Fresenii* and *E. lageniformis*, the position of which in *Empusa* is only provisional. The group is characterized by the production of conidia having a smoky tint, thick-walled, with evenly granular contents and producing peculiar almond-shaped secondary conidia on capillary conidiophores; while its zygospores are elliptical, each originating as a bud which rises upward from the point of conjugation of gametes arising from two hyphal bodies. Further study of *E. lageniformis* may show that these characters, as regards the formation of resting spores, are not sufficiently distinctive. Yet I doubt if this proves to be the case; and, should it prove otherwise, I believe that the subgenus should be separated as a genus from other Empusae.

Under *Entomophthora*, which I have used in brackets as a subgenus, I have included all forms characterized by the production of typically digitate conidiophores; differing from recent German writers in not considering this character of generic value, as well as in omitting even as a subgenus the name *Lamia* given by Nowakowski to a single form (*E. Culicis*).

In his extended paper on Entomophthoreae,[1] Nowakowski summarizes the generic distinctions of *Empusa*, *Entomophthora* and of his genus *Lamia*, as follows:

1. Entomophthora including *ovispora*, *curvispora*, *conica*, and *Aphidis*.
   Fungus growth, one-celled or with filamentous branches.
   Paraphyses, *rhizoids* and *columella*, present.
   Conidiophores, branched.
   Resting spores, zygospores (three species), azygospores (two species).
2. Lamia including the single form *Culicis*.
   Fungus growth, filamentous.
   Paraphyses, present.
   Rhizoids and *columella*, absent (*nie ma*).
   Conidiophores, unbranched.
   Resting spores, azygospores (borne terminally).
3. Empusa including *Grylli*, *Fresenii* and *Muscae*.
   Fungus growth, filamentous.
   Paraphyses and *rhizoids*, absent.
   Columella, present or absent.
   Conidiophores, simple.
   Resting spores, azygospores.

Whether Nowakowski in his text gives more satisfactory characters for the genus *Lamia* than are shown in the above table I am unable to say; but, from the data here given, the presence of paraphyses (which I have apparently overlooked in examining the species) is the single point which separates it from *Empusa* as defined below it. The opinion of Brefeld that the form should be separated as a connecting link between *Empusa* and *Entomophthora*, based upon a tendency to a digitate type observable in the conidiophores and upon the presence of rhizoids is more readily understood, yet singularly enough, and erroneously I think, Nowakowski affirms the absence of both these points of structure. In my own opinion, *E. Culicis* cannot be separated from *E. Muscae* by other than specific distinctions; the points of similarity of the two being decidedly greater than their points of difference. The same may be said of the two species subsequently described as *E. papillata* and *E. apiculata* which bear somewhat the same relation to *E. Grylli* that *E. Culicis* does to *E. Muscae;* each having rhizoids and showing a slight tendency, in the case of *E. apiculata* at least, to a digitate type of conidiophores.

Taking the genus *Entomophthora*, as defined by Nowakowski in the same table, the digitation of the conidiophores is apparently the only exclusive difference of importance which separates it from *Empusa*. Even here *E. Culicis* and *E. apiculata* tend to break

[1] *l. c.* B, p. 176.

down the distinction, as already mentioned. No definite line can be drawn, also, as concerns the production of resting spores; since in species of the *sphaerosperma* type, which must be placed in *Entomophthora*, we have exactly the same type of formation with that occurring in *E. apiculata*, which it is equally necessary to place in *Empusa*. It is true that conjugation is not known in *Empusa* unless it is represented in the very questionable type described under *E. Grylli;* yet it is unsafe to assume that it does not exist, or that its *absence* is of generic value. The only consistent way out of the dilemma consists either in considering all the forms under the tolerably coherent genus *Empusa*, or in resorting to further splitting to express transitional forms. The *sphaerosperma* section of *Entomophthora*, for example, shows decided differences from the rest of the group in the character of its branching, in its conidia and secondary conidia as well as in its formation of resting spores, and may, perhaps, with fuller knowledge of the species already known or subsequently to be discovered, prove separable from the remaining forms. Our knowledge of Empusae is at present in its infancy, and conclusions in respect to subdivisions must be largely based on doubts; a foundation much more likely to produce confusion than a clear understanding of the group.

The use of the name *Empusa* in preference to *Entomophthora* needs a word of explanation, since the two have, until comparatively recent years, been used in the same sense to designate entomogenous Entomophthoreae generally. Although an *Empusa* had been previously described by Fries under an erroneous generic name (*Sporendonema*), the paper of Cohn[1] upon the "house-fly fungus" is the first in which the group was recognized by a generic title, *Empusa*. This publication appeared in 1855, and in the following year Fresenius, in an article[1] preliminary to his more extended paper on the subject,[2] pointed out that *Empusa*, having been preoccupied for a genus of orchids, should be dropped, proposing *Entomophthora* in its place. A few months later Lebert,[3] taking the same ground, proposed the name *Myiophyton*, over which the name of Fresenius of course has priority. The two names have subsequently been used indiscriminately until separated as two distinct genera by Brefeld and Nowakowski, who thus tacitly recognized the validity of *Empusa* as a name; a validity also admitted by Cohn, Eidam, Schroeter and DeBary who employ it without question. If therefore a single name is to be used, *Empusa* certainly has priority and sufficient weight of authority to make its use good. As a matter of fact the orchidaceous genus *Empusa* is placed as a synonym in Bentham and Hooker's Genera Plantarum, and seems unlikely to produce confusion in any case.

The position of the Entomophthoreae among the Zygomycetes is placed beyond a doubt by the formation of the resting spores above described, yet it is interesting to note that, until the publications of Nowakowski, and even subsequently, there has been much difference of opinion concerning their true position; the weight of opinion assigning them a place among the Oosporeae. The theory that the members of the group were merely stages in the life-history of Saprolegniae, which has been maintained on a basis of actual experiments as well as their supposed connection with the yeasts (*Saccharomyces*), is manifestly incorrect and a matter of historical interest only. In the latter case it is of interest to note that species of *Saccharomyces* very frequently occur in connection with

[1] *l. c.* A. [2] *l. c.* B. [3] *l. c.*

Empusae in aphides and flies, the one class of hosts usually having a sweet secretion and the other preferring sweet substances as food, thus supplying a nutritive medium for the growth of yeasts in connection with the *Empusa*. It has occurred to me that the frequent presence of yeasts in this connection might indicate a sweetish secretion from the *Empusa* itself in order to attract hosts for infection; but I have seen no indications that this is the fact.

A natural arrangement of the species of *Empusa* is a matter of great difficulty, since their characters do not, I think, indicate a single line of development. In the succeeding enumeration, for example, the two forms included under *Triplosporium* can hardly be properly placed either at the beginning or at the end of the remaining series, and their position between *Empusa* proper and *Entomophthora* is equally unsatisfactory. The near relations of the forms described as *E. Caroliniana* and *E. Lampyridarum* is also a matter of doubt which may perhaps be removed by further study. A list of the remaining species found in Europe and not yet distinguished in this country, with brief characters and references, is appended for the convenience of students and includes, I believe, all published names not previously referred to. References given as *l. c.*, *l. c.* **A**, etc., refer, as in the previous pages, to the appended list of papers consulted where full titles and references are given.

EMPUSA Cohn, 1855.

Empusa Muscae Cohn.

Pl. 14, figs. 1–9.

Empusa Muscae, Cohn *l. c.* **A**. Brefeld *l. c.* **A**; *l. c.* **B**, p. 28; *l. c.* **C**. Schroeter *l. c.*, p. 221. Nowakowski *l. c.* **B**, p. 176.

Entomophthora Muscae, Fresenius *l. c.* **A**, p. 883; *l. c.* **B**, p. 202, figs. 1–23. Giard *l. c.*, p. 358. Sorokin *l. c.* **C**, p. 195, figs. 377, 582–585. Winter *l. c.*

Myiophyton Cohnii, Lebert *l. c.*

?*Sporendonema Muscae*, Fries *l. c.*

Conidia bell-shaped or nearly spherical, with a broad subtruncate base and sharply pointed apex; $18 \times 20\mu - 25 \times 30\mu$; containing usually a single large oil globule, and surrounded after discharge by a mass of protoplasm. *Conidiophores* simple, broad and stout, tapering gradually to a narrow base; emerging in white rings between the segments of the host, without coalescing over its body. *Secondary conidia* like the primary, or more commonly subovoid, small, rounded at the apex and formed by direct budding from the primary form. *Resting spores*, azygospores, produced laterally or terminally from hyphae within the host; spherical, colorless, 30–50μ in diameter (Winter). Host attached to substratum by proboscis.

Hosts. Diptera: *Musca domestica*, *Lucilia Caesar*, *Calliphora vomitoria* and other large flies; also Syrphidae of several genera.

Habitat. United States, Europe, South America.

This familiar *Empusa* is as common as it is widely distributed, and is at present the only species known south of the equator. It is probable that it is as universal as its more usual host (*Musca domestica*); since, if not indigenous in remote localities, its transportation by sea would be almost inevitable. As a rule, the species is found about houses, usually within them, occurring in great abundance from the latter part of June until late in the autumn; yet its occurrence out-of-doors is an exceptional phenomenon and has been noticed in only a few cases. This is the more singular, since hosts that are liable to infection are very common in the open air, and a transmission to them of the disease from the house-fly would seem a very easy matter. Isolated examples of *E. Muscae* are, however, almost never found in situations frequented, for instance, by *Syrphus* flies, although Cornu[1] records an extensive epidemic in which the hosts attacked belonged to this genus. In my own experience I know of only two instances of the isolated occurrence of this species out-of-doors. The first was observed early in July on Mt. Washington where two small specimens of *Syrphus* were found on bushes in the alpine region, both of which were infested by *E. Muscae;* and in the second instance a specimen of a small, yellow-bodied *Syrphus* was found at Albany in August on the flowers of *Solidago* by Mr. A. F. Chatfield, and forwarded to me, the host in this case being attacked by the same *Empusa.* Mr. Chatfield informs me that it was the only specimen observed, and although I have searched with great care for similar specimens, I have never seen a second instance of the kind. An epidemic in the open air, caused by *E. Muscae*, I have, however, observed in one locality where a hairy black fly (*Anthomyia sp.*) about as large as *M. domestica*, was found killed by this fungus. This locality was the region in the immediate vicinity of the snow arch at the head of Tuckerman's ravine, on Mt. Washington, where the affected flies occurred sticking in large numbers to the flowers of *Solidago* and *Heracleum.* These flowers were also visited by an abundance of other flies, among them many examples of the same species of *Syrphus* previously mentioned from Mt. Washington and Albany; but in no instance did I find one of these or of the numerous other Syrphidae and Muscidae visiting the flowers, that showed any signs of infection from the black flies with which they could hardly have failed to come in contact. This failure of certain species to contract the disease, although known to be subject to it, is interesting as indicating that even a slight change of hosts among *Empusae* is often difficult, until the fungus has become established to some extent in its new conditions, and may go far to explain the difficulty experienced in cross infection subsequently mentioned under *E. Grylli* and *E. sphaerosperma.*

The species is readily distinguished by its pointed, bell-shaped spores which, although entirely similar to those of *E. Culicis*, are much larger. The probable rupture of the columella has been previously alluded to (p. 144) and the surrounding pellicle of protoplasm gives a characteristic appearance to spores which, for example, have been discharged upon a glass slide (figs. 5–6). One of the chief points of interest about the species is the uncertainty that exists concerning its resting spores, which, although the form is so universal have as yet been observed in only one instance. Winter[2] states that he discovered specimens of *M. domestica* in-doors which contained resting spores, and also produced conidia which he identified as belonging to *E. Muscae.* It seems quite impossible that Winter should have mistaken the conidia of any other species for those of *E. Muscae;* yet this observation, although referred to, is not credited by Brefeld, who concludes

[1] *l. c.* B. [2] *l. c.*

that the species never produces resting spores and is continued over winter in warmer regions, whence it migrates northward with the flies on the return of summer. This theory, however, does not coincide with my own experience of *E. Muscae* in this country; since the first specimen which I observed at Cullowhee, where *M. domestica* literally swarmed, was observed at about the same date at which it usually appears in the north, namely July first. For three weeks previous to this date I saw no specimens at Cullowhee; and although I have found not the smallest trace of resting spores in a single instance, it seems improbable that the migration theory can apply to this country at least.

Giard[1] also states that he found resting spores, which were produced externally, occurring on specimens found in cool situations; but it is difficult to determine from his description whether the bodies described are true resting spores, and the observation needs confirmation. On plate I, fig. 7 and plate II, fig. 12, of Lebert's paper,[1] this author has also figured bodies that seem to be resting spores at an early stage of their formation.

The literature concerning *E. Muscae* is very voluminous; the first description of the form having been given by DeGeer in 1782, according to Brefeld; and for further references to this literature the elaborate papers of Cohn, Lebert and Brefeld above cited should be consulted. Whether the first supposed description accompanied by a distinctive name, that of Fries,[1] really applies to the present species is, I think, extremely doubtful; for the oil globules in *E. Muscae* could hardly have given rise to the expression "flocci fertiles erecti, ... intus sporidiis globosis referti," whereas in species of the *ovispora* type, this error of observation might readily have occurred.

Empusa Culicis A. Braun.

Pl. 14, figs. 10–16.

Empusa Culicis, A. Braun *l. c.*, p. 105.
Entomophthora Culicis, Fresenius *l. c.* **B**, figs. 44–45.
Lamia Culicis, Nowakowski *l. c.* **B**, p. 173, figs. 99–114.
Entomophthora rimosa, Sorokin *l. c.* **A**, p. 146; *l. c.* **B**, p. 393, Taf. XIII, figs. 12–19 (with cut); *l. c.* **C**, p. 231, figs. 595–596, 575, 576, 603; *l. c.* **D**, p. 58, plate I, figs. 1-13. Nec *E. rimosa*, Schroeter *l. c.*, p. 222.
?*Saprolegina minor*, Kützing *l. c.*, p. 157.

Conidia bell-shaped or nearly spherical with a broad subtruncate base and sharply pointed apex; $8 \times 10\mu - 15 \times 16\mu$, average $11.5 \times 12\mu$; usually containing a single large oil globule, and surrounded after discharge by a mass of protoplasm. *Conidiophores* simple or with a tendency to become compound; broad at the apex and gradually tapering to a narrow base; producing white or greenish masses which may or may not coalesce over the body of the host. *Cystidia* present (Nowakowski). *Secondary conidia* like the primary, or ovoid with rounded apex and formed by direct budding from the primary spore. *Resting spores*, azygospores, produced laterally or terminally from hyphae, spherical, colorless, 25μ (? in diameter). Host attached by rhizoids.

[1] *l. c.*

Hosts. Diptera: imagines of *Culex* and numerous genera of minute flies or gnats.
Habitat. Maine, New Hampshire, Massachusetts, Europe.

This is apparently the smallest of all the Empusae and is reported to be common in various parts of Europe. Although not previously accredited to this country, I have found it repeatedly in the localities above mentioned. At Kittery, Maine, it occurred early in July on very minute Diptera, adhering to the under side of the leaves of hop, hollyhock and other plants growing about houses; and isolated specimens were found in similar positions in the neighboring woods, or marshy places. Although mosquitoes (*Culex*) abounded in these localities, the only specimen of this insect that I have seen infested with *E. Culicis* was found on the edge of a small brook in the alpine region of Mt. Washington. In this same locality, at the head of Tuckerman's ravine, I have found an insect also attacked by *E. Culicis*, whose reputation is perhaps worse even than that of the mosquito, namely the "black fly" (*Simulium molestum*). These specimens were also found upon the under side of leaves, as in the case of the examples from Kittery; although in Europe the more usual habitat seems to be such moist situations as are afforded by the margins of brooks or the borders of tanks, in which, also, infected specimens may often be found floating.

The form described by Sorokin as *E. rimosa* seems certainly to belong to this species, as has been pointed out by Nowakowski, although Sorokin, in his later publications, still adheres to the opinion that his species is distinct. In describing *E. rimosa*,[1] Sorokin states that the host is attached by rhizoids, and that the conidiophores appear on the thorax, seldom on the abdomen of the hosts, producing bell-shaped conidia of which, so far as I have seen, he gives no measurements in any of his publications. The resting spores he describes as of irregular outline, produced laterally on internal hyphae, which subsequently thicken, contract and, bursting the body of the insect, assume a vertical position on the outside. He also remarks that, from the brief description of A. Braun, it is difficult to say how far the two species (*E. rimosa* and *E. Culicis*) are distinguished. The figures of Fresenius from material received from Braun are, however, good, and correspond to those of Sorokin in Cohn's Beitrage.[2]

As regards the "stroma," which Sorokin describes in this species, I have been unable to satisfy myself; but where the fungus has developed with tolerable luxuriance I have found a condition very like that which he describes; namely, a mass of septate, anastomosing, empty hyphae filling the body of the insect. In other cases, however, I have observed the presence of spherical hyphal bodies or of chlamydospores (fig. 15), which germinated and, after more or less branching, produced conidiophores in the usual way. The resting spores are unknown to me, although I have frequently found small flies containing resting spores in company with the conidial form. In these cases the constant association with specimens of *E. sphaerosperma* on similar hosts has made it impossible to determine to which species the resting form belonged. According to the description of Sorokin above quoted the resting spores would seem to be quite peculiar; yet Nowakowski figures spores of the usual type borne terminally on long hyphae.

[1] *l. c.* C, p. 231. [2] *l. c.* B, Taf. XIII, figs. 16–18.

Empusa Grylli (Fresenius).

Pl. 14, figs. 17–48.

Entomophthora Grylli, Fresenius *l. c.* **A**; *l. c.* **B**, p. 203, figs. 24–43. Sorokin *l. c.* **C**, p. 211, fig. 653. Farlow, Ellis Exsiccati N. A. Fungi, No. 1401.

Empusa Grylli, Nowakowski *l. c.* **B**, p. 168, figs. 72–98. Schroeter *l. c.*, p. 222.

Entomophthora aulicae, Reichhardt in lit. (see Bail *l. c.*). Cohn *l. c.* **B**, p. 77. Sorokin *l. c.* **C**, p. 212. Schroeter *l. c.*, p. 221.

Entomophthora Calopteni, Bessey *l. c.*; Ellis Exsiccati, No. 1801.

Conidia ovoid to pear-shaped, with a broad papillate base and evenly rounded apex; 30–40μ × 25–36μ; hyaline and containing one or more large fat globules. *Conidiophores* simple, coalescing externally when growing luxuriantly, and arising directly from rounded irregular hyphal bodies, with or without subsequent branching. *Cystidia* wanting. *Secondary conidia* of one kind, like the primary. *Resting spores* spherical, colorless; 30–45μ in diameter; produced terminally or laterally from hyphae, directly within or by budding from hyphal bodies; or by a pseudo-conjugation between two divisions of a single hyphal body. Host attached to substratum by the contraction of its legs.

Hosts. Lepidoptera: larvae of many genera of Arctians and of *Orgyia nova*. Orthoptera: larvae, pupae and imagines of many genera of Acridians. Imago of *Ceuthophilus*. ? Diptera: larvae and imagos of Tipulidae, etc. (see *E. conglomerata*).

Habitat. Maine, New Hampshire, Massachusetts, New York, Washington, D. C., North Carolina, Ohio, Iowa, Newfoundland, Europe.

As will be observed, by the synonymy given above, I have included under this species the two forms described as *E. aulicae* and *E. Calopteni*. The description of the first-mentioned species by Cohn[1] is, I believe, the first mention of this name that is accompanied by any note which would render a determination possible. There can be no doubt, I think, that the form common in this country on hairy caterpillars is the same species described from Europe on similar hosts, since the American form agrees with the European in all respects as far as can be ascertained from published data. Assuming this identity, a comparison of the form on caterpillars and the still more common form on grasshoppers, can hardly fail to afford convincing proof that the two represent a single species, their general structure, development and appearance being the same, or varying within similar limits.

I have observed numerous epidemics of the grasshopper form at Kittery in Maine, near Boston and in North Carolina; and the caterpillar form seems also very common, assuming, Mr. Howard informs me, an epidemic character among the *Hyphantria* larvae which have recently done considerable damage to the shade trees in Washington.

In the summer of 1886, I found an epidemic early in September among grasshoppers that were destroying the second crop in a field at Kittery, and also noticed a number of Arctian larvae similarly affected in an adjacent garden. Being struck with the similarity between the two, I endeavored to transfer the disease from the grasshoppers to caterpillars, and for this purpose placed a larva of *Spilosoma virginica* and several of

[1] *l. c.*, p. 78.

Hyphantria textor in a jelly tumbler, and fastened above them a grasshopper from which the spores were being rapidly discharged. These larvae were then fed for eight days in a closed jelly tumbler, at the end of which time the *Spilosoma* had died, and, soon after being placed in a moist chamber, produced a luxuriant growth of conidiophores. In the meantime all of the *Hyphantria* larvae had died from insect parasites, with the exception of two which spun cocoons after a few days. I was entirely unable to transfer the disease from caterpillars to grasshoppers; but I was quite as unsuccessful in infecting grasshoppers from grasshoppers. The reinfection of caterpillars I found more easy, although about two-thirds of the caterpillars used for this purpose showed no signs of the disease and pupated as usual. I was unable to repeat the experiment of cross infection with any satisfactory result, owing to the fact that it was impossible to obtain caterpillars in any number, or good material of *E. Grylli* with which to infect them: I was obliged therefore, in a second experiment, to use larvae of *Pyrrharctia isabella* which were in the hibernating condition. Of five larvae used, one died in eight days and contained resting spores; while the rest were not affected after several weeks. I do not consider these experiments as in the smallest degree conclusive in themselves; but a comparison of other species shows that the hosts of Empusae may be widely different in the same species, and therefore a specific distinction, which, as in the present instance, would rest entirely on the character of the host, should not be considered of any value, even if my experiments did not show that the hosts may be, to a certain extent, interchangeable.

I have been much surprised at the difficulty encountered in communicating the disease among similar hosts, although in the case of grasshoppers this may be perhaps accounted for from the fact that I used only imagines, which may afford a less ready entrance to the germinating spores than younger stages of these insects. In the case of the hairy caterpillars, however, I see no reason why infection should not have been successful in every case. A specimen of *Ceuthophilus*, found at Kittery, which was discharging spores in great quantities, was also used in an attempt to infect three individuals of the same species which were confined with it in a small tin box. The living crickets were put into the box late in the afternoon when the spore discharge was at its height, so that several hundred spores at least must have come in contact with each specimen. On the following morning the living crickets were not only well powdered with spores, but had eaten about half of the infected specimen. Nevertheless, after having been kept for more than two weeks, they showed no signs of the disease. In view of these facts, it is not surprising that my success in cross infection should have been so incomplete, and it may reasonably be assumed that so radical a change of hosts is probably a somewhat gradual process even in nature, the fungus, as has been already noted, requiring one or more generations to become firmly established under its new conditions of nutrition.

Since the species is so widely distributed and generally abundant, there seems to me no good reason for believing that the resting spores described as *E. Calopteni* and found in *Caloptenus* at Ames, Iowa, belong to a different species; and I have therefore placed this as a synonym. Through the kindness of Professor Farlow, I have been enabled to examine authentic specimens of *E. Calopteni* collected by Professor Bessey which differ in no respect from the usual resting spores of *E. Grylli*. Professor Farlow has also allowed me to examine material of *E. Grylli* received from Professor DeBary, and there can be no question concerning the identity of the American and European forms. The occurrence of the species in Newfoundland, where I found it on the larva of *Orgyia nova* on the Salmonier river, should also be noted; since this is, I think, the most northern locality in America from which Empusae have been recorded.

Morphologically, the species is chiefly of interest from the pseudo-conjugation already described on p. 149. I have not had an opportunity of studying the process by cultivations of hyphal bodies; and the figures which represent it (figs. 31–39) are drawn from specimens which occurred simultaneously in a single grasshopper. The process is not uncommon, occurring chiefly in the femora; but in all cases the usual azygospores are by far the most abundant form of resting spores. The production of a double spore by the incomplete union of the two halves of a hyphal body is not infrequent, resulting in forms similar to that represented by fig. 47, in which the union was nearly complete. It sometimes occurs also that there is no union between the two halves, and an azygospore is formed on either side of the median partition. The most common mode by which azygospores are formed is that represented in fig. 43, where the spore is the result of direct budding from the usually irregular hyphal bodies. I have never seen in the caterpillar or in the grasshopper form a process of this kind which is wholly comparable with that figured under *E. conglomerata* (figs. 60–61), for in this case the hyphal bodies are very regular, nearly round, and bear the spores on a short neck. This process is, moreover, invariable in the *Tipula* form as far as I have seen and shows none of the variations which occur in *Grylli*. The same process is figured by Nowakowski,[1] but it is not stated in the explanation of the plates whether these figures are drawn from material on grasshoppers or gnats. The budding, from an arachnoid hyphal body, of spores, which in the explanation of his plates[2] Nowakowski calls "*zygospores*," I have observed in only two cases; but as there seems no indication in this of a sexual process, and Nowakowski in his synoptical table of the species[3] places *E. Grylli* under "Azygospora," I infer that the use of "zygospory" in this connection is a printer's error. A very common form, which I have seen frequently in cultivations of hyphal bodies in water, is that represented in fig. 40, where the spore results from a terminal enlargement of the hypha of germination. A formation from septate hyphae, as in fig. 45, I have seen only once or twice; but the septation as well as the anastomosis and short projections associated with it has, I think, no significance. The occurrence of resting spores is about equally common in caterpillars and in grasshoppers, and the association with them of conidia developed from the same specimen, frequently occurs. The conidia as a rule show little important variation in size or shape, the caterpillar form showing sometimes a tendency to taper more gradually to a slightly broader base than in the grasshopper form; but, on the other hand, I have never seen this tendency so marked in caterpillars as I found it in the spores obtained from the *Ceuthophilus* above mentioned (figs. 25–26).

The earliest occurrence of this species that I have noticed was at Cullowhee, N. C., where I found a single specimen early in July. On the grassy summits of Roan Mt., N. C., it was epidemic in August and also in mowing fields at Cranberry, N. C. An epidemic observed in September at Kittery has already been mentioned; and the latest

[1] *l. c.* B, fig. 94. [2] *l. c.* B, p. 182. [3] *l. c.* B, p. 176.

occurrence that I have noticed was among caterpillars in Cambridge late in October. The tendency of the affected hosts to crawl upwards before death, instead of concealing themselves, as one would naturally expect, is noticeable in this, as in other Empusae, and results in a far more effective dissemination of the spores. The *Ceuthophilus* above mentioned, which usually lives under logs and in similar situations, had crawled up a bush about six feet high and hung suspended from the topmost twigs; grasshoppers also almost invariably crawl nearly to the top of the culms of grass before death, and are thus very conspicuous and easily collected. Mr. Miyabe informs me that he has seen grasshoppers in this position in Japan; but whether the *Empusa* by which they were attacked is *E. Grylli* or not, I am unable to say.

For some mention of European epidemics caused by "*E. aulicae*" which have been noticed as far back as 1835, reference should be made to the papers of Cohn and Bail already cited.

Empusa Tenthredinis (Fresenius).

Pl. 15, figs. 49–55.

Entomophthora Tenthredinis, Fresenius *l. c.* **B**, p. 205, figs. 51–58. Sorokin *l. c.* **C**, p. 212, fig. 652.

Conidia broadly ovoid, tapering slightly towards the apex and with a prominent, rather narrow papillate base; $25 \times 35\mu - 35 \times 55\mu$ (62.5μ = maximum length, sec. Fresenius). *Conidiophores* simple, coalescing over host. *Secondary conidia* like the primary. *Resting spores* unknown. Host attached to substratum by its legs. Rhizoids not observed.

Hosts. Hymenoptera: larvae of Tenthredinidae.

Habitat. Kittery, Maine; Europe.

I have referred to this species a form found early in September upon a small *Tenthredo* larva feeding upon *Scutellaria* in a swampy situation among woods. The larva when found was hanging flaccid by its prolegs, and the conidiophores were just beginning to emerge in small tufts over its body. The spores are somewhat smaller than those described by Fresenius, nor is their difference from *E. Grylli* as decided as represented in Fresenius' plate. A slight tendency to taper more equally from the middle of the spore towards the base and apex, as well as its usually more delicate papilla, may separate it from *Grylli* to which it is closely allied. It is apparently rarely met with even in Europe, the only mention that I have seen beyond that of Fresenius being a reference by Cornu[1] to an *Empusa* on *Tenthredo* larvae. The reference and figure in Sorokin[2] are taken from Fresenius.

Empusa conglomerata (Sorokin) ?.

Pl. 15, figs. 56–62.

Entomophthora conglomerata, Sorokin *l. c.* **A**; *l. c.* **B**, p. 388, Taf. XIII, figs. 1–11; *l. c.* **C**, p. 228, figs. 574, 594, 592.

? *Empusa Grylli*, Nowakowski (in part) *l. c.* **B**, p. 168.

[1] *l. c.* **A**, p. 189. [2] *l. c.*

Conidia broadly ovoid, usually with a single large oil globule; $22 \times 25\mu - 25 \times 40\mu$; average $23 \times 32\mu$. *Conidiophores*, simple. *Secondary conidia*, like the primary. *Resting spores*, azygospores, produced from spherical hyphal bodies and borne on a neck-like process of variable length. Host floating on water, or among moss in water.

Hosts. Diptera: larvae and imagines of Tipulae.

Habitat. Mt. Washington, N. H.; Cullowhee, N. C.; Europe (on Culex).

It is with great hesitation that I have referred to this species a form found in the small brooks which arise in the locality known as the Alpine Garden on Mt. Washington and also very rarely at Cullowhee. In the former locality, the *Tipula* larvae were very frequently met with among moss over which water was running. These larvae were dead having a milky color, and after being placed upon slightly damp moss which absorbed the excess of moisture from them, produced conidia with great rapidity; but in not very considerable quantities. On examination, the body was found in every case to be filled with resting spores in various stages of development, and the conidiophores were present in such small numbers that a "stroma," such as is described by Sorokin in this species, would not have been apparent. The conidia closely resemble those of *E. Grylli*, and usually contain a single large oil globule in the centre. The difference in habitat between *E. Grylli* and the present form is certainly very great, and it is doubtful if *E. Grylli* would survive soaking in running water for a week or more as is necessarily the case with the *Tipula* larvae above mentioned. The regular production of resting spores from nearly spherical hyphal bodies is not such as is found in *E. Grylli* and this is the only morphological difference that I have been able to find between the two. Whether material in good condition and free from resting spores would show the "stroma" of Sorokin, remains to be determined; but judging from the spores figured by this author,[1] as well as by the host and habitat, the present form at least approaches very nearly to *E. conglomerata*. Sorokin gives no measurements of the conidia that I have been able to find, but should the measurements correspond, the conidia of the two forms would be indistinguishable. Sorokin states that the conidium is discharged together with a body of protoplasm from the basidium, a circumstance which, in the examination of dried material, I have not been able to verify in the present instance.

In the plates of Nowakowski[1] certain of the figures of *E. Grylli* are drawn from material on *Culex*, and this author is inclined to think that *E. Grylli* and *E. conglomerata* are the same. The figures referred to do not wholly corroborate this view and it may be mentioned that one among them[2] exhibits the same regular formation of resting spores from spherical hyphal bodies that I have represented in figs. 60 and 61.

Empusa apiculata, nov. sp.

Pl. 15, figs. 63–70, 74–75.

Conidia nearly spherical, with a prominent papillate base, terminating in a short, sharp and abrupt point; $28\text{–}30\mu \times 30\text{–}37\mu$, average $30 \times 35\mu$. *Conidiophores* simple, sometimes with a tendency to become digitate, originating directly or indirectly from nearly

[1] *l. c.* **B.**

[2] *l. c.* **B**, Plate XI, fig. 94.

spherical hyphal bodies. *Secondary conidia* like the primary. *Resting spores*, azygospores or zygospores(?), formed laterally or terminally from hyphae, spherical; hyaline, 30–45μ. Host attached to substratum by long and conspicuous rhizoids, few in number and terminating in an irregular, disc-like expansion.

Hosts. Lepidoptera: larva of *Hyphantria textor*, imagines of *Tortrix* sp., Deltoid sp., *Petrophora* sp. (geometrid). Diptera: numerous genera of small flies or gnats. Hemiptera: imago of a species of leaf hopper (*Typhlocyba*).

Habitat. Maine and North Carolina.

Var. **major**.

Pl. 15, figs. 71–73.

Conidia more nearly spherical; $38 \times 45\mu - 55 \times 60\mu$; basal papilla smaller in proportion to the body of the conidium than in the typical form.

Host. Coleoptera: imago of *Ptilodactyla serricollis* (*fide* Henshaw).

Habitat. Cullowhee, North Carolina.

It is with some reluctance that I have given a new name to this form, although by the presence of strong rhizoids and by its apiculate papilla it seems a well-marked species. The existence of three allied species, *E. Jassi*, *E. Planchoniana* and *E. conglomerata*, concerning neither of which is any information procurable beyond the insufficient data already published, makes the description of a related form necessarily dangerous, so that the present name is in a measure provisional until more complete descriptions or figures of the three forms mentioned are published. The case is rendered still more confusing by the occurrence on aphides of the species described below and placed provisionally under *E. Planchoniana*. This may prove to be the same with the form under consideration, and both may be identical with *E. Planchoniana;* yet, what the latter species is, it is wholly impossible to determine from published data.

In the present species we have the first recorded instance of an *Empusa* growing upon a lepidopterous imago as its host, although, as will be subsequently seen, this is not an unique case. The geometrid moth, above mentioned as one of its hosts, was taken on the wing, flying slowly with an unnatural fluttering motion and being placed in a collecting box it was soon fastened to a leaf by five or six long and powerful rhizoids. These on examination were found to be made up of several hyphae each ending in an irregular expansion (fig. 75) around which a hyaline substance seemed to have been secreted, converting it into a disc-like sucker. Where several of these terminations had touched the leaf at adjacent points the several expansions usually coalesced to form one large "sucker," with a continuous even outline formed by the secretion just mentioned. This moth contained both conidia and resting spores, the latter forming in a manner exactly resembling that subsequently mentioned under *E. sphaerosperma*. The appearance of a resting spore having its origin in connection with a cross partition, as in fig. 74, occurred occasionally and seemed wholly analogous to the similar appearance in *E. sphaerosperma* (figs. 214–216).

The conidiophores, in many instances, arise directly from nearly spherical or elliptical hyphal bodies (fig. 64); but in some cases I have observed a condition where the body has been filled with a coherent mass of empty, interlacing hyphae resembling the "stroma" described by Sorokin and previously referred to. The conidiophores, which are clear white, coalesce over the body to a great extent, forming an envelope of considerable thickness. They sometimes tend to become digitate, so that this species, together with *E. Culicis*, forms a connecting link between the simple and compound types.

The species occurs not uncommonly in North Carolina on the under side of leaves in *Rhododendron* thickets; and I have found it occasionally in Maine near brooks or marshy places in woods, always on leaves. The specimen on *Hyphantria textor* (larva) was found at Burbank, E. Tenn., in one of the nests peculiar to these caterpillars; but, although there were many in the nest, I found no additional specimens attacked by the fungus. The omnivorous character of the species is noticeable, and experiments with infections of different hosts are much to be desired, especially with aphides, since it is only by this means that the true relations between this and the succeeding form can be determined.

Empusa Planchoniana (Cornu)?.

Pl. 15, figs. 76–78.

Entomophthora Planchoniana, Cornu *l. c.* **A**, pp. 189, 190; *l. c.* **B**, foot-note, p. 4. Sorokin *l. c.* **C**, p. 214.

Conidia nearly spherical or broadly ovoid, with a papillate base which is sometimes furnished with a short sharp point. Average measurements 28–33μ × 30–40μ. *Conidiophores* simple, partially coalescing over the host. *Secondary conidia* like the primary. *Resting spores*, azygospores, produced laterally or terminally, more commonly interstitially, from hyphae; spherical, or very irregular in the interstitial forms; 35–50μ in diameter. Host attached to substratum by the insertion of its proboscis.

Hosts. Hemiptera: several genera of aphides.

Habitat. Kittery, Maine; vicinity of Boston, Mass.; Europe.

It is with much hesitation that I have placed under the above name a species occurring in this country commonly, yet never very abundantly, on numerous aphides infesting the white birch, *Bidens* and other plants, in late summer and autumn, associated as a rule with other species which attack the same hosts. It is sometimes found also associated with *E. Aphidis* in greenhouses where it may be found during the winter months. It is very nearly related to *E. apiculata*, and, if not a variety of this species, forms a connecting link between it and *E. Grylli*. It differs from *E. apiculata* chiefly in the absence of rhizoids, which I have been unable to discover in fresh material after a careful search, as well as by the variability of its conidia which are rarely pointed as in *E. apiculata*, and vary from a form nearly spherical to one not separable from that of even the longer forms of *E. Grylli*. The species may be placed under *E. Planchoniana* only provisionally as may be understood from the following descriptions of the last named species by Cornu.

In speaking of the species,[1] Cornu says that the conidiophores, issuing from the body

[1] *l. c.* **A**.

of the aphides, "donnèrent naissance a une sphérule mucronée, remplie d'un plasma réfringent et au centre de laquelle apparaisait une spore en forme de toupie d'Allemagne. Dans l'air humide les sporanges furent lancés au loin," etc.: and in the only other place where I find the species characterized,[1] he says "Cette espèce parait characterisée par la production . . . de spores *ovoïdes oblongues*, sans sporanges, ou sporanges soudés à la spore" (the italics his). I am unable to reconcile these two descriptions or to determine whether the author here realizes what I consider to be the true morphology of the *Empusa* conidium. The phenomenon of the separation of the outer wall I have never seen in the round spored species of the "*Grylli*" type to which the present form belongs, and such a separation so exceptional in any case, that its occurrence as a characteristic of the general morphology of any species is highly improbable. A "sphérule mucronée" may refer to a conidium of the "*Muscae*" type; yet since the conidia are characterized as in the form "de toupie d'Allemagne" as well as "ovoïdes oblongues" this seems doubtful. The last expression perhaps refers to another species on aphides (the common *E. Aphidis*); yet any opinion concerning the form to which *E. Planchoniana* belongs is purely conjectural, since the above quotations which furnish all the published data concerning the species are not of such a nature as to render its determination possible.

Empusa papillata nov. sp.

Pl. 15, figs. 82–90.

Conidia broad-ovoid, evenly rounded, with a very large tongue-like slightly truncate papilla, clearly defined from the spore body. Average measurements $35 \times 50\mu$, maximum $50 \times 75\mu$. *Conidiophores* stout, simple. *Secondary conidia* like the primary. *Resting spores* azygospores (?), 45–55μ in diameter, spherical, slightly brownish. Host attached to substratum by a few large rhizoids, terminating in a sucker-like expansion.

Hosts. Diptera: several minute gnats.

Habitat. Mt. Washington, N. H.; Cullowhee, N. C.

I first noticed this species on the wet *Sphagnum* surrounding a spring in the locality known as the Alpine Garden on Mt. Washington, where it occurred in July and August (1886). I also found a small number of specimens on very minute gnats in the beds of mountain brooks at Cullowhee, in company with several other species, which occurred on moist logs and in similar situations. The conidia sometimes attain a size greater than any other *Empusa* known to me and are peculiar for their prominent tongue-like papillate base. They are formed usually in small numbers and are visible to the naked eye without difficulty. Like *E. apiculata*, this form is peculiar for its few powerful rhizoids which attach the host firmly to the moss or other substratum on which it rests. It differs from the last-mentioned species in its much larger conidia which are of a more ovoid shape, while it apparently lacks entirely the sharp point peculiar to the basal papilla of *E. apiculata*. It is not impossible that the form on *Culex* referred by Nowakowski to *E. Grylli* may be the present species; yet, as previously mentioned, I am inclined to think that he refers to the species I have called *E. conglomerata*. The two forms, *E. conglomerata* as above described and the present species, are, I think, quite distinct.

[1] *l. c.* B.

The resting spores of this species occurred in several specimens simultaneously with conidia, but were in every case too far advanced in their development to demonstrate their process of formation, which can hardly vary greatly from that of the nearly allied *E. apiculata*.

Empusa Caroliniana nov. sp.

Pl. 16, figs. 91–105.

Conidia ovoid, oblong or long elliptical, with rounded extremities, the base hardly separable from the apex; without large oil globules; measuring $10 \times 26\mu - 15 \times 45\mu$, average $14 \times 37\mu$. *Conidiophores* simple, barely projecting beyond the body of the host between the body segments and from the thorax; originating directly from rounded hyphal bodies. *Secondary conidia* like the primary. *Resting spores* (azygospores) spherical, hyaline, 37–55μ in diameter, average 45μ (?). Host attached to substratum by its legs.

Hosts. Diptera: imagines of *Tipula* sp.

Habitat. North Carolina.

This species is decidedly different from any form known to me and is easily recognized by its shapeless conidia which, although they are of the *Entomophthora* rather than *Empusa* type, are borne on conidiophores which are rarely branched within the body of the host and are perfectly simple at their extremities; the hyphae swelling directly to a basidium upon emerging. Specimens producing the fungus with the greatest luxuriance may therefore show little indication of its presence, and in dried material it is almost wholly invisible, the body segments closing over the basidia in shrinking. A single specimen only was taken at Cullowhee, while at Cranberry I procured a considerable amount of excellent material. The affected insects (a brown *Tipula* with mottled brown wings) were found in a small group of hemlocks among deciduous woods and occurred invariably hanging from the lower dead twigs, about which the extremities of their long legs were knotted in such a manner that it was impossible to disengage them. Several specimens contained only hyphal bodies and I was thus enabled to see the greatest possible development of conidiophores, by placing the *Tipulae* in a moist atmosphere. Other specimens produced both conidia and resting spores, although I was unable to make out the origin of the latter. As far as could be judged from the examination of material in which the process was already completed, it consisted in a budding from rounded hyphal bodies, but no satisfactory observation was possible in any case. The terminal and interstitial production of hyphal bodies (fig. 92) through the successive contraction of the contents of branching hyphae was frequently observed; but in other cases rounded hyphal bodies occurred, associated with resting spores, which were much larger than those represented in the figure and may have had a different origin.

Empusa (Triplosporium) Fresenii Nowakowski.

Pl. 16, figs. 106–140.

Empusa Fresenii, Nowakowski *l. c.* B, p. 171, Pl. XII, figs. 115–125. Schroeter *l. c.*, p. 222.

Conidia nearly spherical to short-ovoid, often with a short, truncate or commonly slightly papillate base; with granular contents; without large fat globules, and slightly smoky in color; $15 \times 18\mu - 18 \times 20\mu$. *Conidiophores* simple, arising directly from small, spherical hyphal bodies of a yellowish color. *Cystidia* not observed. *Secondary conidia* of two kinds: the first like the primary, the second almond-shaped and borne obliquely on capillary conidiophores. *Resting spores*, zygospores, elliptical or subovoid, yellowish, becoming often smoky and opaque, formed by the conjugation of two small, spherical hyphal bodies by means of slender gametes, above the point of junction of which the spore rises as a bud; average measurements $30 \times 19\mu$. Host attached to substratum by the insertion of its proboscis.

Hosts. Hemiptera: *Aphis mali* and very many other aphides.

Habitat. Maine, Massachusetts, North Carolina, Europe.

The name adopted above for this interesting species is that used by Nowakowski in his Krakow paper[1], although, to avoid confusion, it should be mentioned that the same author in his review of this publication[2] uses the name "*Freseniana*" by an apparent oversight. The species is a very common one, having been found by Nowakowski on numerous aphides and also recorded by Schroeter as belonging to the Silesian flora. Although it has not been previously noticed in America, I have found it very common at Kittery, Maine, in the vicinity of Cambridge and also as far south as Cullowhee, N. C., where both the conidial and zygosporic forms occurred on an *Aphis* infesting *Solidago*. At Kittery, a black *Aphis* on poppy, as well as the common apple *Aphis*, was found attacked by *E. Fresenii* about the middle of June; and the last mentioned host contained abundant zygospores even at this early date. I have found the same species on aphides infesting *Bidens* and other plants about Cambridge as late in the season as the first week of October; but here no resting spores occurred. The formation of the resting spores, illustrated by the series of figures (127–140), has already been described in some detail (p. 148). As far as can be determined from alcoholic or dried material, the masses of protoplasm (figs. 106–108) from which the conjugating hyphal bodies are derived, have no proper wall, a circumstance which has been previously noted by Sorokin in connection with his *E. colorata*. Before reproduction commences, these protoplasmic masses become divided, rolling themselves into small, spherical hyphal bodies (fig. 127), which, when developing, certainly show the presence of a surrounding wall. This wall, during the process of conjugation, becomes considerably thickened, so that the two hyphal bodies remain attached to the spore in the form of bladder-like appendages which are tolerably persistent (figs. 135–138). The zygospores, which have been hitherto unknown, differ from all other described forms by their elliptical shape. In very mature specimens, they are sometimes almost black and opaque, though I am unable to say whether this is due to the absorption of coloring matter from the host; or whether, as seems more probable, the resting spores may not assume a smoky color, analogous to that of the conidia, which is deepened by age.

The conidia are readily distinguished by their small size and smoky tint, as well as by the peculiar almond-shaped secondary conidia of the second type, borne on slender,

[1] *l. c.* B. [2] Bot. Zeitung, XL, p. 561.

thread-like conidiophores, which may be seen produced from them abundantly in any preparation, the ordinary form of secondary conidia being of rare occurrence. The primary conidia possess more than usually refractive, homogeneous contents, in which are embedded numerous fine granules; and the thickness of the spore wall is noticeable as in the succeeding species, although in the present instance it is not indicated in figs. 110–116. The growth of the fungus is never luxuriant, and each spherical hyphal body, from its small size, can hardly give rise to more than one or two conidia.

As already mentioned, I have taken this and the succeeding species (*E. lageniformis*) as the types of a new sub-genus, *Triplosporium*, which will, I think, prove to have a generic value when further information has been obtained concerning the development of the last-named species.

Empusa (Triplosporium) lageniformis nov. sp.

Pl. 16, figs. 141–160.

Conidia slightly smoky, flask-shaped, with a truncate, hardly papillate base, rounded apex and evenly granular contents; average measurements $20 \times 35\mu$, maximum $30 \times 38\mu$. *Conidiophores* simple, or when young sometimes fasciculate or pseudodigitate; terminating by a weak, tapering basidium. *Cystidia* not observed. *Secondary conidia* like the primary, or almond-shaped and borne obliquely on capillary conidiophores. *Resting spores* unknown. Host attached to substratum by the insertion of its proboscis.

Hosts. Hemiptera: usually aphides on *Betula populifolia*.

Habitat. Maine, Massachusetts, North Carolina.

The discovery of the resting spores of this species is perhaps the most interesting fact that remains to be observed among American Empusae, owing to its undoubted affinity with *E. Fresenii*. The species being of larger dimensions than *E. Fresenii*, we may look for an instance of true conjugation which may be even more readily followed than in the last mentioned form. I have found only scattered examples of this species in single localities, although it is generally distributed in company with *E. occidentalis*, subsequently described. Both forms occur, as far as I have observed them in New England, only upon a large *Aphis* generally found in abundance on the white birch in August and September. Numerous specimens examined contain no signs of resting spores, producing only conidia which are similar to those of *E. Fresenii*, except as regards their larger size and somewhat peculiar shape. The single specimen collected at Cullowhee occurred on an *Aphis* infesting *Solidago*, so that it is probable that the disease could be readily propagated among greenhouse aphides, for example, and thus afford a means of observing its further development.

Empusa (Entomophthora) Lampyridarum nov. sp.

Pl. 17, figs. 161–172.

Conidia regular, ovoid; slightly tapering towards the apex; with an abrupt, broad, slightly papillate base; contents granular, without large oil globules. Measurements

$14 \times 30\mu - 20 \times 37\mu$, average $15 \times 35\mu$. *Conidiophores* digitate (?). *Secondary conidia* like the primary or more commonly long-cylindrical, rounded at either end, and borne *vertically* on capillary conidiophores. *Resting spores* unknown. Host attached to leaves, etc., by its mandibles.

Hosts. Coleoptera: imago of *Chauliognathus Pensylvanicus.*

Habitat. Cullowhee, N. C.

This interesting species was unfortunately not observed by me until a day or so before leaving Cullowhee, so that my material is limited to two specimens in fair condition, yet not sufficiently good to determine definitely the character of the conidiophores which, I have little doubt, are typically digitate. The specimens were allowed to discharge their conidia in a damp chamber so that the conidiophores were apparently exhausted by the operation; and those remaining were of the character represented in fig. 161. The secondary conidia of the second type are very peculiar, and separate the species at once from all others by their vertical position upon the conidiophore, as well as by their peculiar shape which is exactly that of a watermelon.

In the absence of more definite knowledge concerning the structure of the conidiophores, as well as from the lack of material containing resting spores, the affinities of the species are somewhat doubtful. It seems allied both to *Triplosporium* and to the *sphaerosperma* group of *Entomophthora;* but the type of development in its resting spores must be observed before this can be determined.

The melon-shaped secondary conidia are produced in great abundance, even in a fairly moist atmosphere, and in only one or two instances I observed a second form like the primary conidium in process of formation. In many cases, the more common secondary conidia were larger than the spores from which they were produced, and this, together with the apparent thinness of the spore wall, seems to indicate that they are not as resistent as is usually the case with secondary conidia when borne on capillary conidiophores. It will also be noticed that the secondary conidiophores are much less thread-like than is usually the case.

The affected beetles (fig. 172) were found firmly attached by their mandibles to grass or leaves in open fields; and, to judge from the number of heads that I observed in this position from which the bodies had been broken away, I should infer that the species had been not uncommon in the locality mentioned. The same beetle was abundant at Burbank, E. Tennessee, yet here I observed no specimens of the *Entomophthora.*

Empusa (Entomophthora) geometralis nov. sp.

Pl. 17, figs. 173–178.

Conidia short-elliptical to ovoid; $15–22\mu \times 10–12\mu$; contents finely granular, with a hyaline nuclear body. *Conidiophores* digitate, coalescing. *Cystidia* not observed. *Secondary conidia* like the primary, or long almond-shaped and borne obliquely on capillary conidiophores. *Resting spores* borne laterally or terminally on short hyphae as in *E. sphaerosperma;* spherical, colorless, average diameter 30μ, maximum, 35μ. Host attached to substratum by numerous rhizoids issuing from the abdomen at nearly the same point, and for the most part coalescing.

Hosts. Lepidoptera: imagines of geometrid moths (*Petrophora*, *Eupithecia*, *Thera*, etc.).

Habitat. Kittery, Maine.

This species was found during the month of September (1886) attacking geometrid moths of several species in or near pine woods, a favorite habitat of these insects. It is usually the habit of the host to rest with the abdomen curved upwards and, at one point of the under surface, resting on whatever object the moth may have lighted upon, usually a pine needle. At this point of contact, and, as far as I have observed, nowhere else, the rhizoids are produced in a tuft which thus fastens the insect by its abdomen. The rhizoids appear before death and I have found a small *Eupithecia* fluttering violently in its efforts to free itself from a pine needle to which the rhizoids had already become firmly attached (fig. 173). Although the specimens collected were found for the most part on the borders of pine (*P. strobus*) woods, several were noticed in other situations, as for instance, in a room used by me for collecting night moths by means of a lamp. Here several specimens of *Eupithecia*, thus attracted, were found fastened to the walls and window panes. The species was not studied while fresh and none of the dried specimens were in the proper condition for showing clearly the method by which the resting spores are formed. As far as could be seen, however, the process is similar to that described in *E. sphaerosperma*.

The conidia are peculiar and may be at once recognized by their short, thick form, which readily distinguishes them from those of the closely allied *E. sphaerosperma*.

Empusa (Entomophthora) occidentalis nov. sp.

Pl. 17, figs. 179–199.

Conidia of the *sphaerosperma* type, sometimes slightly fusiform, often tapering strongly towards the apex, with a broad, rounded, papillate base. Average measurements $35 \times 10\mu$, maximum $45 \times 12\mu$. Contents usually finely granular, sometimes with larger fatty bodies. *Conidiophores* irregularly digitate, coalescing in a white or slightly yellowish mass. *Cystidia* slender, slightly tapering. *Secondary conidia* like the primary, or long almond-shaped and borne obliquely on capillary conidiophores. *Resting spores*, azygospores or zygospores (?), borne laterally or terminally by budding from the hyphae; colorless, spherical, 20–35μ in diameter. Host attached to substratum by numerous rhizoids.

Hosts. Hemiptera: aphides on *Betula populifolia*.

Habitat. Maine, Massachusetts.

This is a well marked species of the *sphaerosperma* type, and occurs very commonly on the aphides which usually infest the common white birch in late August and in September. It generally is associated with the much rarer *E. lageniformis* which attacks the same host, and it may be found, in my experience, in almost any locality where the white birch grows. The conidia are chiefly noticeable from such forms as are represented by figs. 183 and 184 which strike the eye at once in examining a preparation. The contents of the conidia are usually finely granular with a central nuclear body (figs.

185–189); but sometimes contain fatty globules of considerable size. The resting spores often occur in specimens also producing conidia, and are commonly formed by lateral budding from short hyphae in an apparently non-sexual fashion; but numerous instances occur, as in *E. sphaerosperma*, where the budding is associated with a partition, as in figs. 196, 198–199, which may perhaps indicate a sexual process. In a few cases spores developing from long hyphae growing in the legs seemed to result from a process which may with safety, I think, be considered a form of conjugation (fig. 197).

The species has little that is peculiar in its structure and is only interesting as being another example of the strongly marked *sphaerosperma* type.

Empusa (Entomophthora) sphaerosperma (Fres.).

Pl. 17, figs. 200–219.

Entomophthora sphaerosperma, Fresenius *l. c.* **A**, p. 883; *l. c.* **B**, p. 207, Taf. IX, figs. 68–78. Sorokin *l. c.* **C**, p. 220, figs. 579–81, 586–90, 632–33, 654. Schroeter *l. c.*, p. 223.
Tarichium sphaerospermum, Cohn *l. c.* **B**, p. 84.
Empusa radicans, Brefeld *l. c.* **A**; *l. c.* **B**, p. 14, Taf. I–II.
Entomophthora radicans, Brefeld *l. c.* **C**; *l. c.* **D**. Nowakowski *l. c.* **A**; *l. c.* **B**, p. 165, Taf. X, figs. 63–67, Taf. XI, fig. 71.
Entomophthora Phytonomi, Arthur *l. c.* **A**; *l. c.* **B**.

Conidia long-elliptical to nearly cylindrical; papillate at base and tapering very slightly near the rounded apex; $15–26\mu \times 5–8\mu$, average $20 \times 5.5\mu$; usually with a fine granular contents and a central oval nuclear body. *Conidiophores* much branched and confluent over the body of the host, forming usually a mass the upper surface of which is flattened. *Conidiophores* digitate. Color of the fungus as a whole white, varying to bright pea green. *Cystidia* slender, tapering, not abundant. *Secondary conidia* like the primary, or long almond-shaped and borne on a capillary conidiophore. *Resting spores*, azygospores or zygospores (?), borne laterally or terminally from hyphae; $20–35\mu$, average 25μ; spherical, hyaline or very slightly yellowish. Host attached to substratum by rhizoids.

Hosts. Lepidoptera: imago of *Colias philodice;* larva of *Pieris.* Hymenoptera: Ichneumonidae of several genera and species, a small bee (near *Halictus*). Diptera: imago of *Musca domestica* (Brefeld), *Musca sp.* (Roan Mt., Thaxter); numerous small species belonging to the Culicidae, Mycetophilidae, Tipulidae and other families. Coleoptera: larva of *Phytonomus punctatus;* imago of one of the Lampyridae. Hemiptera: *Aphis sp.*; several species of *Typhlocyba* (leaf hoppers), larvae, pupae and imagines. Neuroptera: imago of *Limnophilus* (?) (Schneider). Thripidae: larvae, pupae and imagines of a species of *Thrips* on *Solidago.*

Habitat. Maine, New Hampshire, Massachusetts, New York, North Carolina, Europe.

It is unnecessary to remark that this species is peculiar for the great diversity of its hosts which include all insect orders, excepting only the Orthoptera. It is an extremely common form, probably from this reason, and often produces epidemics of considerable proportions. It was first reported from this country by Mr. J. C. Arthur who describes it as *Entomophthora Phytonomi* n. s., having found it destroying the clover weevil (*Phytonomus punctatus*) in great numbers in the vicinity of Geneva, N. Y. The affected larvae, just before death, crawl up blades of grass, etc., and curling themselves around them near the summit are attached by the rhizoids in this position. Material of the *Phytonomus* form received by me from Professor Riley, which was collected, I believe, by Professor Lintner at Albany, N. Y., shows no sufficient differences which can separate it from the same form on other hosts, although the average measurements of the conidia are very slightly larger than in the majority of cases, the maximum length given by Arthur being 28μ, while as a rule I have seldom found it more than 25μ. The shape of the spores is identical with that which characterizes the other forms and is similar to the published figures of *E. sphaerosperma* to which all the forms occurring on the hosts above enumerated should, I feel confident, be referred.

In my own experience, I have observed two epidemics caused by this species: one among certain small flies in a wood near marshy ground at Kittery, Me., where the hosts occurred in considerable numbers fixed by the fungus on the under side of the lower leaves, a few feet from the ground. The second instance occurred in two orchards in the same locality where the hundreds of the previously mentioned epidemic were replaced by tens of thousands, the host in this instance being the leaf-hopper (*Typhlocyba mali* and *rosae*), a pest only too well known to cultivators of roses. Having first observed it in some abundance on roses in a garden, I was led to make an examination of adjacent apple orchards, and found the lower branches of the trees literally covered with the affected hosts, a dozen or more being often fastened to a single leaf. Unfortunately, I was too late, and in almost all cases the specimens had discharged their spores, while no more hosts remained for infection. A few, however, were still producing conidia, and it occurred to me to endeavor to infect from them the larvae of *Pieris*, which is the common European host of this species. For this purpose I placed a small number of young larvae in the bottom of a jelly tumbler, fixing the infected hosts above them as previously described. This was on Sept. 10 (1886); on Sept. 16, the majority had prepared to pupate, the larvae having been too far advanced when infected. One larva, however, on the evening of the sixteenth, was found dead and attached to the leaf on which it had been feeding by powerful rhizoids which issued from the region of the prolegs. This larva was not disturbed for twenty-four hours, in the hope that conidiophores might make their appearance, but none appeared, and the insect became slightly collapsed. Upon examination, it was found to contain numerous, spherical resting spores, about 25μ in diameter, the origin of which could not be seen, all traces of hyphae having disappeared owing to a partial decomposition of the contents of the caterpillar which also contained several larvae of *Pteromalus*. This fact surprised me greatly, since, in his infection experiments, Brefeld states that no result was produced when spores were sown on larvae thus infested. A double parasitism was also found in my experiments with *E. Grylli* previously mentioned, in which the larvae of certain insect parasites issued from several caterpillars thickly covered by conidiophores. The remaining larvae in the present experiment died with *Pteromalus* or pupated within a day or so. Several died from *Pteromalus* after pupation, and the remainder, three or four in number, died before or after pupation and were found to contain irregular bodies resembling hyphal bodies, but often without apparent walls and associated with a general fatty degeneration of the whole contents of the pupa. At this date (Sept. 17) it was only possible to procure very poor material for infecting a fresh set of *Pieris* larvae, and although much younger larvae were selected than in the previous experiment, no results were obtained; the caterpillars upon reaching maturity either dying from insect parasites or pupating.

Although these experiments by themselves are not by any means convincing, the infection of even a single *Pieris* larva from a host so totally different, and under circumstances such as I have described, when taken in connection with the structural similarity existing between the American and European forms, furnishes in my opinion sufficient ground for considering them as belonging to a single species.

The occurrence of this species on a butterfly (*Colias philodice*), fig. 200, is also an interesting fact; the specimen in question, which was found on the ground in a pasture at Kittery, being, I believe, the first recorded instance of this nature. This is also I think, the only species that has been found to attack hymenopterous imagos, on which it very commonly occurs; a fact that might be of interest to bee-raisers, should the fungus develop a local fondness for bees. In this connection it may be noted, however, that several hives of bees placed under the trees in the apple orchards above mentioned, showed no signs of any entomophthorous disease.

The species probably has a very wide geographical range, and although in North Carolina I have found it less common than in New England, it occurred in some quantities on a fly, somewhat smaller than *Musca domestica*, which I found fixed to the under sides of the leaves in *Rhododendron* thickets on the summit of Roan Mountain. On Mt. Washington, N. H., I have found it infesting flies, ichneumons, and a minute *Thrips* which it destroyed in great numbers. This occurrence upon *Thrips* is interesting as illustrating the omnivorous character of the parasite. Krasilstchik, in his list of insect hosts attacked by fungi, gives *Thrips* as the host of an undetermined species of *Entomophthora* which is, I believe, the only other recorded instance of this insect as an *Empusa* host. The infested larvae, pupae and imagines of this insect, as they occurred on Mt. Washington, were hardly visible without a hand lens. Both conidia and resting spores occurred in this instance; the former somewhat smaller and more irregular than in the case of hosts whose size admits of a more luxuriant growth of hyphae, yet differing but little from the usual type.

The general appearance of the fungus in this, as well as in the succeeding species, when it is well developed on its smaller hosts, is almost always sufficiently peculiar to distinguish it from other Empusae. The whole mass of conidiophores coalesces over the body often leaving only the middle of the thorax uncovered; but instead of presenting the rounded form usual in other Empusae, the upper surface has a flattened appearance, and is the only portion from which conidia are discharged. This is due to an oblique tendency observable in the growth of the main hyphae, as is indicated in fig. 202, the left hand portion in the figure corresponding to the outer part of the whole mass. The basidia thus have a general tendency to point upwards instead of in all directions as is usually the case. The occurrence of specimens in which the mass of conidiophores is colored green or greenish is not common, and the color fades on drying; but in two cases in the epidemic among leaf hoppers just mentioned, I found specimens in which it was colored a vivid pea green, a circumstance that can hardly be due to any coloring matter from the host, which is of a pale yellowish tint. A similar coloring will be noticed presently under *E. dipterigena*.

The formation of the resting spores in this species has already been mentioned (p. 147). The instances figured (figs. 214–217) were taken from two leaf hoppers, the only specimens that I have examined in which the development of the spores was at exactly the proper point for observing their origin. The differences apparent between this process and that figured by Brefeld[1] are, in my opinion, merely the result of the difference existing between the conditions present in either case; the totally dissimilar nature of the host being in itself a sufficient explanation. It should be noticed also that in the legs of these same specimens the hyphae were long and continuous, and, although no resting spores had begun to develop in them, an occasional anastomosis was apparent; while the same is true of the preceding species (*E. occidentalis*) in which resting spores were observed in a similar situation in connection with hyphae which showed anastomoses here and there.

Empusa (Entomophthora) Aphidis Hoffman.

Pl. 18, figs. 220–240.

Entomophthora Aphidis, Hoffman in Fresenius *l. c.* **B**, p. 208, figs. 59–67. Winter *l. c.* Sorokin *l. c.* **C**, p. 213, figs. 593-594, 634; *l. c.* **D**, p. 60, plate II, figs. 14–18. Nowakowski *l. c.* **B**, p. 164, figs. 59–62.

Tarichium Aphidis, Cohn *l. c.* **B**, p. 84.

Entomophthora ferruginea, Phillips *l. c.*, p. 4, plate III, figs. 1–13.

Conidia ovoid to elliptical or subfusiform; commonly asymmetrical and very variable; with papillate base and containing numerous oil globules. Average measurements $25 \times 12\mu$, maximum $16 \times 40\mu$. *Conidiophores* digitate, often simple. Hyphal bodies spherical, germinating in all directions and giving rise to numerous contorted hyphae which grow into conidiophores. *Cystidia* rather slender and tapering at their extremities. *Secondary conidia* like the primary, or short ovoid with a single large oil globule. *Resting spores* "spherical, 33–45μ in diameter and borne terminally or laterally on hyphae" (Fresenius and Sorokin). Host attached to substratum by rhizoids, few in number, and usually terminating in a disc-like expansion.

Hosts. Hemiptera: Aphides of numerous genera.

Habitat. Maine, New Hampshire, Massachusetts, N. Carolina, Washington, D. C., Europe.

It is of course impossible to determine whether the description of Fresenius[2] really refers to this species or to other forms found upon aphides and producing similar resting spores; yet there can be no doubt that the conidia first described by Winter[3] and subsequently described and figured by Nowakowski are identical with those of the form above described. Although I have not myself observed the resting spores of this species, they are described by Winter and Sorokin as spherical, so that the assumption is justified that in the present instance we are dealing with the true *E. Aphidis*, which must

[1] *l. c.* D. [2] *l. c.* B. [3] *l. c.*

otherwise be distributed among at least four other species having spherical resting spores and growing upon aphides, namely, *E. sphaerosperma*, *E. occidentalis*, *E. Planchoniana* and the form under consideration. I have, it will be noticed, placed *E. ferruginea* as a synonym of this species, although Mr. Phillips states that his species, in the opinion of Mr. Cook, is a distinct form, as shown by a comparison with authentic specimens of *E. Aphidis.* The figures and descriptions of *E. ferruginea*, however, as far as I can judge, point to the present species; and moreover the exsiccati specimens of *E. Aphidis* are unreliable, the two numbers that I have examined[1] containing in the one instance nothing whatever, and in the other *E. Fresenii*, a species which cannot be confounded in any way with *E. Aphidis* on account of its peculiar resting spores.

Although this species (*E. Aphidis*) has not, to my knowledge, been previously reported from the United States it is, with the exception of *E. Muscae* and perhaps *E. Grylli*, the commonest of all the Empusae; occurring abundantly in the localities above mentioned. It was first called to my notice by Dr. George Dimmock who noticed it in a greenhouse in Cambridge during the winter of 1886. In this situation it acted as a decided check to the multiplication of the aphides, yet did not spread with sufficient rapidity to render "smoking" in the greenhouse unnecessary. At Kittery I have found it on numerous genera of aphides and especially destructive to the forms which injure the hop. In one case I observed a large hop vine some twenty feet high completely covered with aphides which were killed off by this fungus in about two weeks; the affected hosts being fastened to the under sides of the leaves, and to the younger shoots in vast numbers. The destruction of colonies of *Aphis* by this species or by *E. Fresenii* seems to be the rule rather than the exception, and is at least of very common occurrence. An instance of the kind was called to my attention during the second week in June of the past year (1887) by Mr. L. O. Howard, who showed me great quantities of aphides dying of the disease on clover near the agricultural department buildings in Washington. The probable agency of ants in spreading these epidemics is worthy of notice as well as that of night moths, especially *Noctuidae*, which, as well as ants, are often attracted in great numbers by the sweet secretion of the aphides.

Despite the abundance of the conidial form, I have never obtained a single specimen of the resting spores that I have been able to discover among my material. The conidial form is chiefly of interest from the peculiar "germination" of the hyphal bodies represented in fig. 239, and consisting in the production, from a central cell with a highly refractive contents, of a mass of hyphae growing from it in all directions, and subsequently giving rise to the conidiophores. This at least is the usual derivation of the mass of contorted and branched hyphae which may be found filling the aphides just before the external appearance of the conidiophores. The number of these cells or hyphal bodies is small, as may be inferred from the enormous number of hyphae which each produces, and their origin is a question which I have been unable to settle from actual observation; although in a few cases I have found large hyphae at a less advanced stage of the development of the fungus, the contents of which were collected terminally or interstitially into rounded masses which may have represented the hyphal bodies in question.

The conidia are noticeable from their considerable range of variation, both in size and

[1] Myc. Univ. No. 1916; Herb. Myc. No. 768.

shape. The conidiophores are white in the mass, often tinged with yellowish or flesh color from the coloring matter of the host, which usually assumes a pale brick-red tint at or just before death. This change of color is, however, common to most aphides attacked by Empusae and cannot be considered distinctive of any species. In one instance I have found a form, apparently this species, on a large bug (one of the *Corisiae?*); but, unless the species subsequently described as *E. dipterigena* proves to be the same fungus, there is little variation from the usual host.

Empusa (Entomophthora) dipterigena nov. sp.

Pl. 18, figs. 241–250.

Conidia variable in shape, ovoid to oblong or subfusiform, with a papillate base, often bent to one side, and containing numerous large oil globules; average measurements $11\times22\mu$, maximum $15\times30\mu$. *Conidiophores* digitate coalescing over the body of the host in a clear white, very rarely bright pea green mass. *Cystidia* slender, tapering toward the apex. *Secondary conidia* like the primary or broad-ovoid. *Resting spores* (zygospores?) produced *externally* in grape-like clusters; spherical, hyaline, 20–40μ in diameter. Host attached to substratum by rhizoids; few in number, large, with a disc-like terminal expansion.

Hosts. Diptera: small Tipulae; other small flies or gnats belonging especially to the Mycetophilidae.

Habitat. Maine, New Hampshire, Massachusetts, North Carolina.

Before discovering specimens of this species producing both the conidia and resting spores simultaneously, I was inclined to regard it as a mere variety of *E. Aphidis;* but the peculiar external production of the resting spores, taken with its generally smaller measurements and quite different host, serves sufficiently to distinguish it. It is nearly allied to *E. ovispora* and *E. echinospora*, but separable at once from the first by its slender tapering cystidia, and from the second by its smooth resting spores. From *E. Americana* it is separable by its smaller, often subfusiform conidia, as well as by the presence of cystidia, its general habit and peculiar rhizoids.

None of the specimens found contained resting spores at a sufficiently early stage of their development to show the nature of their origin. The youngest examples, in which the spore contents were still granular, indicated a tendency to produce distinctly grape-like clusters, and in all cases the spores were external. The species is not uncommon, occurring only on the under side of leaves in woods or thickets, and was first noticed on Mt. Washington in late August, at the head of Tuckerman's ravine, and subsequently collected in swamps about Kittery, Maine, in small numbers. In North Carolina, it was more common in similar situations, both forms of spores occurring not infrequently.

I have placed the *E. rimosa* of Schroeter[1] as a doubtful synonym of this form, with which his description coincides with little variation. Schroeter's species is certainly not the *E. rimosa* of Sorokin, the spores of which belong to a very different type.

[1] *l. c.*

Empusa (Entomophthora) virescens nov. sp.

Pl. 18, figs. 251–261.

Conidia ovoid to oblong, of irregular shape; with bluntly rounded base and apex, the former often hardly papillate and not well distinguished from the apex; color greenish yellow in dried material; containing numerous small, irregular, often rod-like fat bodies; measurements $10\times20\mu$–$16\times36\mu$, average $14\times30\mu$. *Conidiophores* digitate, arising indirectly from spherical hyphal bodies which germinate in all directions, giving rise to very numerous hyphae which subsequently become conidiophores. *Cystidia* not observed. *Secondary conidia* like the primary. Resting spores unknown. Host attached to substratum by rhizoids?

Hosts. Lepidoptera: larvae of *Agrotis fennica.*

Habitat. Ottawa, Ontario (Mr. Fletcher).

The specimens from which the above description was taken were received by Professor Farlow from Mr. J. Fletcher, Dominion entomologist, who writes concerning them as follows:—"In the spring of 1884 from May 15 until the end of the first week in June, all the gardens and fields in the district around Ottawa were severely attacked by the larvae of *Agrotis fennica.* The disease of which you have a specimen was first observed about the 22nd of May, and was extremely virulent. Dead larvae were to be found in all directions; on stone walls, on fences and particularly on the tops of stems of grasses. They were also vigorously assailed by Tachinidae and Carabidae. The *Entomophthora*, however, was undoubtedly *the* influence which brought this insect down again to its normal rare occurrence at Ottawa." The specimens received were black and shrivelled, the fungus appearing as a greenish yellow coating, emerging in small tufts, which, in the more mature specimens, appear to have coalesced over the body. The conidia appear also greenish yellow in the mass, and are recognized by their general shapelessness and rounded extremities, as well as by the numerous small fatty bodies of a crystalline appearance which characterize the spore contents. I have placed this species near *E. Aphidis* from the structural similarity indicated by the peculiar germination of the hyphal bodies already described in the last-named form; but the conidia seem to be of a different type.

It should be noted that the host of this species is closely allied to that of *E. megasperma* of Cohn which also occurs upon an *Agrotis* larva. Mr. Fletcher writes me that he has not observed a single specimen of the fungus since the date above mentioned, and as the material originally sent contained only conidia I am unable to give any information concerning the resting spores. The conidia of *E. megasperma* are unknown, nor has the species been observed to my knowledge since it was described by Cohn.[2] The resting spores of *E. megasperma* are fortunately an exception to the general rule, being readily recognized by their dark brown, reticulate epispore, so that the question concerning the identity of the present form with Cohn's species can be settled beyond a doubt as soon as the resting spores of the one or the conidia of the other become known.

[1] *l. c.* B.

Empusa (Entomophthora) Americana nov. sp.

Pl. 18, figs. 262–273.

Conidia long-ovoid, with a broad evenly rounded apex; tapering for some distance to a papillate base often slightly bent to one side. Within the spore are usually numerous fatty bodies often very regular in size and shape. Average measurements $28–30\mu \times 14\mu$, maximum $35 \times 15\mu$. *Conidiophores* regularly digitate, arising from large, irregular, roundish hyphal bodies, and coalescing over the host in a mat-like covering which becomes slightly rust colored on exposure. *Cystidia* absent. *Secondary conidia* like the primary. *Resting spores*, colorless, hyaline, spherical; average diameter $38–45\mu$, maximum 50μ. Process of formation not satisfactorily observed. Host attached to substratum by numerous filamentous rhizoids, without terminal root-like expansions; forming an even mat-like attachment continuous around the abdomen of the host.

Hosts. Diptera: *Musca domestica*, *M. vomitoria*, *Lucilia Caesar*, and numerous other large flies.

Habitat. New England and North Carolina.

This common species is frequently met with from June to October on the borders of woods, near brooks or in shrubbery about houses. The host is generally found fixed to the under, rarely on the upper, side of leaves or on bare twigs, a few feet from the ground. It can readily be distinguished by its general habit from any species known to me with the exception of *E. echinospora;* since the rhizoids instead of growing out in the form of numerous scattered threads are developed in an even layer around the hosts' body forming, with the conidiophores, a continuous mat-like covering which becomes often dark rust colored on exposure to the weather. The mass of conidiophores is at first pure white, and in a moist chamber grows with great luxuriance.

The conidia are almost identical in appearance with those figured by Nowakowski as belonging to *E. ovispora* and the measurements are very nearly the same. *E. ovispora* is, however, at once separated from the present species by its peculiar cystidia which resemble those belonging to *E. sepulchralis* (fig. 306). In the present species, I believe there are no cystidia whatever, and I have looked in vain for anything remotely resembling them. Whether the type of conjugation found by Nowakowski in *E. ovispora* exists also in the present species, I am unable to say, since in all cases in which I have found resting spores, the latter were mature and no trace of their method of production was visible. *E. Americana* is also closely allied to *E. muscivora* of Schroeter which seems to be identical with *E. Calliphorae* of Giard. The resting spores in both these instances are described as chestnut or deep chestnut brown; and since the material of both seems to have been abundant, I have no hesitation in separating them from our species in which the spores are always perfectly hyaline. They occur not infrequently in connection with the conidia, and my material is sufficiently large to demonstrate the invariability of their color or lack of color. In North Carolina the species was of rarer occurrence than in New England, and I obtained but few specimens on shrubs in open woods or on twigs of hemlock. It has been taken also by Professor Farlow and Mr. Miyabe at Woods Holl, Mass., and a specimen from New Hampshire which I have not examined microscopically is in Dr. Hagen's collection of entomogenous fungi. I have collected it frequently at Kittery and in the vicinity of Boston, and it has been sent to me from Jaffrey, N. H.

Empusa (Entomophthora) montana nov. sp.

Pl. 18, figs. 274–285.

Conidia, ovoid to turbinate, usually tapering from a broadly rounded apex to a somewhat attenuated, slightly pointed base, containing numerous large oil globules and measuring $11 \times 18\mu$–$15 \times 25\mu$. *Conidiophores* digitate, coalescing over the host in a livid white mass and arising directly from rounded hyphal bodies. *Cystidia* tapering or rounded at the apex, larger than the conidiophores. *Secondary conidia* like the primary or short ovoid. *Resting spores* unknown. Host attached to substratum by numerous rhizoids.

Hosts. Diptera: a minute gnat, apparently *Chironomus* sp.

Habitat. Alpine summit of Mt. Washington, N. H.

This small species was found late in August, 1886, in great abundance on a small gnat common about one of the brooks running into the "Lake of the Clouds" on Mt. Washington; several hundreds of specimens being obtained from the wet *Sphagnum* bordering the brook. I have observed it in no other locality, even on Mt. Washington, although thorough search was made in similar localities in other parts of the mountain. The species presents no peculiarities of interest beyond the shape and size of its conidia which are readily distinguished by their usually pointed base and broad apex which give them the appearance of a long top.

Empusa (Entomophthora) echinospora nov. sp.

Pl. 19, figs. 286–305.

Conidia ovoid, tapering to a papillate base; usually nearly symmetrical; 20–25×10–14μ; containing one or more large oil globules. *Conidiophores* digitate, coalescing into a mat-like covering which turns rust colored on exposure. *Cystidia* not observed. *Secondary conidia* like the primary or varying only slightly. *Resting spores*, zygospores, spherical 30–40μ in diameter, the exospore spinose; commonly produced externally as well as internally, and in the former case held slightly, after maturity, by a delicate mesh of hyphae. Host attached to substratum by rhizoids, coalescent around the abdomen in the conidial form.

Host. Diptera: imago of *Sapromyza longipennis* and rarely other smaller Diptera.

Habitat. Maine, New Hampshire, North Carolina.

A single specimen of this interesting species containing both resting spores and conidia, together with several examples that were useless from exposure, were found in August, 1886, among the alders at the head of Tuckerman's ravine, Mt. Washington, on the pretty yellow-winged fly that appears to be its almost invariable host. The conidia so nearly resembled those of *E. Americana* and *E. dipterigena* that it was only by accident that I examined the specimen a second time after having placed it with my material of these species. Having discovered the peculiarity of its resting spores, I looked for it with some care in North Carolina during the succeeding summer and was rewarded by finding the same host repeatedly infested by the same fungus. In Carolina it occurred almost invariably on the under side of leaves especially of *Impatiens* growing beside brooks in the woods. The conidial form was extremely rare, but of the resting condition I procured some dozens of specimens. In very many cases the resting spores are produced wholly, or more commonly partially, outside the body of the host, having originated from hyphae (fig. 297) which emerge after the manner of conidiophores, and subsequently conjugate as shown in figures 298–302. Certain of these hyphae are seen to project some distance beyond the rest (fig. 297) and ultimately form a delicate web which serves to hold the mass of spores to some extent. None of my material was sufficiently good clearly to show conjugation within the body of the host, and the hyphae were so evanescent and filled with such large globules of fat that points of conjugation could hardly be made out in the confused mass. The spines develop more rapidly within the body than without and as a result of their formation the abdomen becomes greatly inflated. This inflated appearance together with the peculiarity of the host are sufficient to distinguish the species in collecting, and it is a singular fact that this particular species of fly (*Sapromyza*), even in situations where *E. dipterigena* was common and *E. Americana* not infrequent, never appeared to be attacked by any other *Empusa*. The spinose character of the spore is due to elevations of the rather thin-walled epispore only, and is thus readily obliterated by long exposure or transformed into a roughness of the surface. The epispore may also be easily removed by pressure of the cover-glass upon it, disclosing within a spherical resting spore of the usual type. The species is very nearly allied to *E. dipterigena*, the conidia of the two being hardly separable in some cases. The papilla is, as a rule, broader in *E. echinospora* and the spores seldom tend to become fusiform. The type also represented in figures 243–244, which is characteristic of groups of conidia in the former species, is wholly wanting in the latter as far as I have observed.

Empusa (Entomophthora) sepulchralis nov. sp.

Pl. 19, figs. 306–326.

Conidia long-ovoid to long-elliptical or subfusiform, rounded at the apex and with a papillate base commonly bent to one side; hyaline, with numerous large oil globules; measurements 35–48 × 10–15μ, maximum 15 × 55μ. *Conidiophores* digitate, arising from large (60μ diam.) spherical hyphal bodies and coalescing over the body of the host in a clear white mass. *Cystidia* very large (70–90μ in diameter), slightly expanded or commonly becoming branched at their apices. *Secondary conidia* like the primary or short-ovoid. *Resting spores*, zygospores, spherical, hyaline, 35–50μ in diameter; formed as the result of a *Spirogyra*-like conjugation between two hyphae and arising by budding from the gametes. Host attached to substratum by numerous rhizoids.

Hosts. Diptera: imagines of Tipulidae.

Habitat. North Carolina, E. Tennessee.

This fine species was collected at Cullowhee, Cranberry and Burbank from June 20 to Sept. 5 of the past summer (1887), occurring commonly on the largest Tipulae, which were often found in considerable numbers adhering to wet logs or similar objects along the small brooks, so constantly met with in the Carolina mountains. Localities most attractive to the Tipulidae were naturally the most productive of the *Entomophthora* and, in situations where the brooks were obstructed by fallen trees or roots over which they partially flowed, a dozen or more often occurred side by side. A plentiful supply of moisture seems always necessary for the development of the fungus, which is only found on surfaces saturated with water. This circumstance results in a very luxuriant growth of the conidiophores which makes this species the most conspicuous of any form on Diptera known to me. Although the abdomen of the host is usually narrow and not more than a few mm. broad, the conidiophores, after bursting through the integument about the thorax and between the segments, become confluent and spread to some distance on either side of the body forming a clear white mass of considerable dimensions. The effect thus produced is decidedly ghost-like, especially when a number of Tipulidae are seen in this condition beneath a shaded log, and has suggested the specific name.

The species is remarkable from its formation of true zygospores in a fashion similar to that discovered by Nowakowski in his *E. ovispora*, *E. conica* and *E. curvispora*. I was unable to determine that the zygospores were formed from the same hyphae which bear the conidia, as stated by Nowakowski in the species above mentioned, and it seems more probable from my observations that certain of the hyphal bodies develop conjugating hyphae, while others develop conidiophores. I was unable to satisfy myself on this point, since cultivation of the chlamydospores in water produced only conidia; and, in specimens producing zygospores, the hyphae were invariably too much broken up to allow of any definite conclusion in this respect. I found no instances in which zygospores alone were formed and usually the number was comparatively small. They were, however, almost invariably present in greater or less abundance in the considerable number of specimens examined; yet only in a small number of cases did I find them in the early stages of formation. This is apparently due to the great rapidity of the process after it has once begun, since, in several instances, specimens in which no zygosporic formation was visible when first examined, contained perfectly formed zygospores after the lapse of a few hours. The singularly large cystidia are very noticeable and readily seen with the naked eye, the drop of moisture which, as a rule, they bear at their apices giving them the appearance of conidiophores with single apical spores of unprecedented dimensions. The species is allied to *E. ovispora* and *E. conica* as well as *E. rhizospora* with all of which it agrees exactly in the origin of its zygospores. It is perhaps most nearly allied to *E. ovispora* from which, however, it differs by its much larger and differently shaped conidia, which although subject to some variation in size and shape, especially when developed in situations where the supply of moisture is insufficient, are yet tolerably constant at from 40 to 50μ in length. The ease with which the outer wall becomes separated in this species is noticeable in fresh material, and in several instances I observed this phenomenon carried to such an extent that the spore proper floated free within the inflated and spherical mother cell (fig. 321).

It should be noted that the occurrence of this species although common was decidedly local, and in no instance did I find it in company with allied forms at even a short distance from the water.

Empusa (Entomophthora) variabilis nov. sp.

Pl. 20, figs. 327–343.

Conidia usually varying according to the period of their discharge, those first formed being ovoid, short and stout, with a papillate base and broadly rounded apex and measuring about $15 \times 11\mu$. Those formed later are much more elongate, either shaped like a short straight club or strongly curved, and measure $18–30 \times 7–9\mu$, average $25 \times 8\mu$. *Conidiophores* digitate, having in the mass as a rule a distinctly olive tint. *Cystidia* in small numbers, slightly tapering, larger than the conidiophores. *Secondary conidia* like the primary, of two general types. *Resting spores* unknown. Host attached to substratum by numerous rhizoids.

Hosts. Diptera: minute gnats of various genera.

Habitat. North Carolina.

I have found this small species pretty generally associated with *E. conica* in Carolina especially at Cullowhee, where it occurred not uncommonly in the beds of wood-brooks and was found by turning over stones or wet pieces of wood in these situations. It seldom occurs, in any abundance in one locality, and is very difficult to find from the minute size of the insects which it attacks: yet it is almost always recognizable by the olive color of the conidiophores which, though not invariable, usually affords a ready means of separating it from other species with which it may be associated. I know no other species in which a peculiarity in the tint of the conidiophores as a mass serves as a distinguishing character, although the occurrence of a bright green specimen has been noted in *E. sphaerosperma* and *E. dipterigena.* In these cases, however, the colored forms are rare exceptions. The variation of the primary conidia from short-ovoid (fig. 343) to straight or curved forms several times longer than broad (figs. 329–342) is a noticeable feature in this species, and led me at first to separate my material into two sets which I considered distinct species. By allowing the discharge of spores to continue for a longer time I have, however, repeatedly seen the longer form replace the shorter one, and I think there can be no doubt of their specific identity. The secondary conidia of the second type are nowise different from these first formed primary conidia.

The resting spores, I feel confident, I found in one instance; the insect containing them being associated with others bearing conidia. The specimen, which has unfortunately been lost, had produced no conidia so that I was unable to verify this opinion. From memory I can only say that the spores were small in size, decidedly brownish and held together by the hyphae from which they were formed. These hyphae, as in the nearly allied *E. rhizospora*, seemed somewhat indurated: but they were formed internally, and did not produce the rhizoid-like outgrowths which characterize the last named species. The resemblance of this form to *E. curvispora* should be noted, many of the spores closely resembling those figured by Nowakowski as belonging to this species.

Empusa (Entomophthora) rhizospora nov. sp.

Pl. 20, figs. 347–348.

Conidia, in form, like a straight short club, varying to almost crescent-shaped; very variable, tapering more or less at either extremity, the basal portion of the spore neck-like and bearing the rounded papilla of attachment; contents with large fat globules; average measurements 30–35 × 8–10μ, maximum length 42μ. *Conidiophores* digitate, coalescing in a livid white mass over the insect. *Cystidia* large, not numerous, slightly tapering. *Secondary conidia* like the primary, or spherical with an abrupt, delicate papillate base. *Resting spores,* zygospores, spherical, 40–60μ, with brownish epispore; budding from *Spirogyra*-like gametes and subsequently surrounded by rhizoid-like outgrowths which are closely applied to the spore and originate at its base. The hyphae producing zygospores are always *external* and subsequently become thickened and horny, turning dark chocolate brown and holding the spores in a spongy mass. Host attached to substratum by numerous rhizoids.

Hosts. Neuroptera: several genera of Phryganeidae (imagines).

Habitat. Kittery, Maine; and North Carolina.

This interesting form was first observed by me at Kittery, where I found one or two specimens producing only resting spores, under boards or logs in swampy situations. From the peculiarities of its spores and their external formation, I was inclined at first to consider it as the type of a different genus; since none of these specimens were in sufficiently good condition to demonstrate the method by which the spores were formed and the hyphae had already become brown and indurated. In North Carolina, I found both the conidial and the zygosporic form very common, both kinds of spores often appearing on the same specimen. The affected hosts were not, as in the preceding species with which it is commonly associated, exposed in open sight; but, in accordance with the hiding habit of the caddis flies (Phryganeidae), were found concealed under saturated logs or very commonly under stones, partially exposed in the bed of shallow wood streams, or in swampy places in woods. The larvae were also common in the same situations, but I never observed that they were attacked by the fungus.

Although a very large number of specimens were examined I only found a very few in which the process of conjugation was visible, and even in two instances where it had not begun at sundown, I found it completed during the forenoon of the following day so that its details could not be seen. The process is thus, as in the preceding species, a very rapid one. The persistence of the hyphae, concerned in the formation of zygospores and their subsequent modification, is very peculiar as compared with the evanescent character of the hyphae which distinguishes the family in general. The utility of the modification, together with that of the rhizoid-like outgrowths which hold the spore, is quite apparent in this particular case; for, owing to the peculiar habits of the host, the fungus is developed in situations such as those described, in which it is liable to be flooded and washed away at any moment when the water of the brook rises even an inch or so. The thick elastic hyphae, under such circumstances, hold the mass of spores with great tenacity, and the whole is fastened to the substratum by the indurated rhizoids with such firmness that a knife is required to scrape it off. It is probable that the whole collection of zygospores, having hibernated thus, germinate in the spring, growing out into a coalescent mass of conidiophores as in the ordinary asexual type (fig. 377); but, although I found specimens that, from their appearance, must have been in the brooks for several months, no spores were observed that showed signs of germination.

The growth of the conidiophores is very luxuriant, greatly exceeding the size of the host, and extends on either side usually so as to invert the wings, turning them upside down (fig. 377). The color of the mass is more livid than is commonly the case in Empusae and shows no variation towards a greenish hue. The conidia are very variable, usually strongly bent, and are readily distinguished by their neck-like basal portion. The secondary conidia of the second type are remarkably regular in shape (figs. 362–365), and of a type which differs widely from that of the primary spores.

A somewhat remarkable degeneration of the conidiophores was observed in, I think, three instances. The specimens in which this occurred were noticeably different in appearance from the usual conidial form, having a milky color and not presenting the usual appearance of luxuriant growth. On examination the white substance in these specimens proved to be composed of hyphae that had for the most part already broken up into short pieces which were seen to produce at one extremity (figs. 366–367) the singular bodies shown in figs. 368–69, of which the mass covering the insect was chiefly made up. These bodies, which are about the size of the conidia, are almost invariably in the form of an irregular kind of cross, the lateral outgrowths appearing at variable distances from the extremities of the body; but always of about the shape represented in the figures referred to. I saw no sign of any germination in them, though I was unable to make proper cultivations, and I cannot explain their occurrence unless it be due to a degeneration of the mass of conidiophores, which subsequently attempt to fulfil their office in this peculiar fashion. The specimens occurred in the usual situations in company with the normal type, and the cause for the degeneration, if it be such, as well as for the peculiar shape of the resulting bodies is not apparent, nor have I ever seen any condition remotely resembling this in other Empusae.

In the formation of zygospores it should be noted that, unlike the preceding species, the conjugating hyphae are rarely, if ever, septate near the point of union, and are very irregular, running into attenuated branches. The production of a spore from each of the gametes (fig. 369) was sometimes noticed as well as the occurrence of double spores (fig. 373*a*) apparently formed side by side. In one instance (fig. 368) conjugation seemed to have occurred between the apices of hyphae and not by the usual *Spirogyra*-like method.

Empusa (Entomophthora) gracilis nov. sp.

Pl. 21, figs. 379–391.

Conidia slender, subfusiform, with a neck-like papillate basal portion and attenuated apex; strongly curved, rarely straight, containing large oil globules. Measurements 7–9 × 30–45μ, average 40 × 8μ. *Conidiophores* digitate, coalescing over host in a white mass. *Cystidia* of rare occurrence, rounded at the apex. *Secondary conidia* like the primary; or nearly spherical, papillate. *Resting spores* unknown. Host attached to substratum by rhizoids.

Host. Diptera: on very minute gnats.

Habitat. Cullowhee, N. C.

Like *E. variabilis*, with which it is commonly associated, this species seems to attack only the minutest gnats and is thus very difficult to find. A small number of specimens were taken at Cullowhee in July at different times; but I found it in no other locality and it is apparently very rare. The conidia are very slender and readily separated from those of *E. conica* by their fusiform shape, neck-like basal portion and constantly smaller size, the maximum length being slightly over 45μ.

The species has no interest beyond the fact that it affords a second instance of the peculiar "*conica*" type of conidia, and I can give no information concerning the resting spores.

Empusa (Entomophthora) conica Nowakowski.

Pl. 21, figs. 392–410.

Entomophthora conica, Nowakowski *l. c.* **A**; *l. c.* **B**, p. 155, plates VIII and IX, figs. 1–32.

Conidia long, slender, conical, often strongly curved with a rounded papillate base tapering to the usually blunt extremity; 25–80 × 10–14μ. *Conidiophores* digitate, arising as a rule directly from nearly spherical hyphal bodies and coalescing over the body of the host in a clear white mass. *Cystidia* larger than conidiophores, rounded at apex. *Secondary conidia* like the primary or broadly ovoid, rarely pointed at the apex. *Resting spores*, zygospores, produced by a *Spirogyra*-like conjugation, usually budding from one of the gametes; spherical, colorless, 30–50μ in diameter. Host attached to substratum by numerous rhizoids.

Hosts. Diptera: imagines of *Chironomus* and other small gnats.

Habitat. Mt. Washington, N. H., North Carolina, Europe.

The singular shape of the conidia in this and the preceding species distinguishes them at once from all other known Empusae although a transition from the ovoid type to this elongate form is seen in *E. sepulchralis*, *E. variabilis* and *E. rhizospora*. The exact advantage of such a shape it is difficult to understand as the spores do not seem so well calculated to hit and adhere to a passing host as the more blunt forms. In contrast to this elongate form the secondary conidia of the second type are extremely compact, sometimes approaching those of *E. Muscae* in shape. The separation of the conidium proper from the mother cell wall is very commonly seen in this as in other species which vegetate in very moist situations, and the tendency of the spore contents to become more or less contracted is often observable; the contracted portion separating itself from the empty extremity by a cross partition (fig. 396). The conidia themselves vary considerably in size and shape, in the bluntness of their apices which I have never seen as sharply pointed as is represented in Nowakowski's plate, and in the relative thickness of the spore and its amount of curvature. With regard to the curvature of this and other elongate forms, a natural explanation seems to be afforded by the deviation of the conidiophores from a perpendicular position which is usually more or less considerable except in the upper middle portion of the mass. The conidia, while in process of formation, endeavor to correct this deviation by curving upwards thus giving rise to the strongly curved elongate forms as well as to the abruptly bent bases so commonly seen in the *ovispora* type. It is noticeable that this curvature is rarely, if ever seen in Empusae of the *sphaerosperma* type; and the reason for this is very evident in view of the peculiar mode of growth, already described in the last-named species, which characterizes the mass of conidiophores as a whole, and allows the basidia to assume a vertical position which is impossible in the rounded masses of the usual type.

In material of this species, where the growth of conidiophores has not been luxuriant, the form of the conidia may be constantly such as is represented in figures 403–404; in fact the majority of the specimens obtained from Mt. Washington produced spores of this nature. The affected hosts occurred in this locality on moss along the borders of small brooks in the Alpine Garden, and only when the moss was completely saturated with water, allowing an abundant growth of conidiophores, were the spores of the usual elongate type. I have thought this worthy of mention, since the small form might readily be taken for a distinct species. Although occurring in considerable quantities on Mt. Washington, the species is somewhat rare in North Carolina where it is found in company with *E. variabilis* on saturated wood or stones in the beds of brooks flowing through woods. It may be readily distinguished from the last-named species by the clear white color of the mass of conidiophores.

The resting spores I have found in but few specimens, produced simultaneously with the conidia by a process exactly similar to that described in *E. sepulchralis*.

This completes the enumeration of American *Empusae* at present known, and for convenience of reference I have added below a list of the European species which are unrecorded from this country.

European species of Empusa as yet unrecorded from the United States.

Empusa Jassi, Cohn *l. c.* **B**, p. 77. Sorokin *l. c.* **C**, p. 239. Schroeter *l. c.*, p. 222.

This form, of which no complete description has ever been published, is referred to by Cohn (*l. c.* **B**, pp. 76–77) in connection with his account of *Tarichium megaspermum*. In this place he mentions that the spores are spherical and 20μ in diameter, but gives no specific name to the form, which, he states, occurs on *Jassus 6-notatus*. Where the name *Jassi* first originated I am unable to say, and the species cannot be recognized without further information regarding it. It may prove to be the species previously described as *E. apiculata* which has many hosts, and it forms another element of confusion in the group comprising *E. conglomerata*, *E. Planchoniana*, *E. apiculata*, *E. Jassi* and perhaps *E. Tenthredinis*. I quote below the note of Schroeter in his Silesian flora concerning this species.

"330. *Empusa Jassi*, Cohn, 1870. Mycel im Körper von Cicaden lebend, an den todten Thieren als sammetartiger, weisser Schimmelüberzug hervorbrechend. Conidien kugelig, 20μ Dchm.

Auf *Jassus sex-notatus* Mai, Juni.—Die todten Thiere haften den Grashalmen u. s. w. fest an, die vier Flügel wie zum Fluge ausgespreizt.—Breslau Schneitig 1869 in grosse Menge."

Entomophthora colorata Sorokin, *l. c.* **C**, p. 215, figs. 573, 623, 627; *l. c.* **D**, p. 62, Pl. III, figs. 5–6, 19–27, Pl. IV, figs. 28, 28′.

This species which is said to occur on grasshoppers seems to be peculiar from its colored conidial spores which, according to Sorokin, are reddish brown, round and resemble those of *E. Muscae* except in color. The protoplasm from the basidium is discharged with the spore. Sorokin states that it closely resembles *E. Grylli*, differing, however, by its round and colored conidia. It is in this species that Sorokin has observed peculiar amoeboid bodies within the host which produce resting spores laterally or terminally. For some further account of this species a review of Sorokin[1] may be found in Just's Bot. Jahresbericht (1881), p. 292, by Batalin.

Entomophthora Tipulae, Fresenius *l. c.*, **B** p. 206, figs. 46–50. Sorokin *l. c.* **C**, p. 211, fig. 651.

I find no mention of the occurrence of this species since it was described and figured by Fresenius. The conidia are described as ovoid, with a short, broad, rounded, projecting base; measuring 33-40μ in length. The figures represent a broad almost truncate base and ovoid body which gives the spore a characteristic outline. The species was found on a large *Tipula* which was wingless and adhering to a rush. The mass of spores and hyphae had a greenish brown color. The form should be readily recognized by the large size and peculiar shape of its spores, yet I have seen nothing like it on similar hosts in this country.

Entomophthora Calliphorae, Giard *l. c.*
Entomophthora muscivora (*E. Calliphorae* Giard?), Schroeter *l. c.*, p. 223.

The species described by Giard on large flies (*Calliphora*) can, I think, hardly be distinct from the *E. muscivora* of Schroeter since the rare peculiarity of a deep chestnut-brown (*marron foncé*) resting spore, the measurements of which are the same (30μ in *Calliphorae* and 24–28μ in *muscivora*) is common to both. The hosts and habit correspond in the two forms, *E. muscivora* differing only in the fact that its conidia are also described, while in *E. Calliphorae* they were not observed. Schroeter describes the conidia of his species as ovoid, with a blunt papilla; 20–24μ long by 11–13μ broad. On large flies which are attached by numerous rhizoids. The conidia are slightly smaller than in the form that I have described as *E. Americana* from which it is separated by the peculiarity of the resting spores.

Entomophthora ovispora, Nowakowski *l. c.* **A**; *l. c.*, **B**, p. 160, figs. 33–58. Sorokin *l. c.* **C**, p. 235.

The conidia of this species almost exactly resemble those of *E. echinospora* and *E. Americana*, being somewhat long-ovoid with papillate base and rounded apex. Like *E. Americana* they contain numerous small oil globules of very regular size; but the species is at once separated from either of the forms just mentioned by its peculiar cystidia which are very large, resembling those of *E. sepulchralis* (fig. 306). The conidia measure from 22μ to 28μ in length by 14μ in breadth. The resting spores are zygospores produced by a *Spirogyra*-like conjugation and are of the usual type, 31μ in diameter. The species occurs on flies: *Lonchaea vaginalis*, *Syrphidae*, *Sapromyza*, *etc.*, and is found in wet situations on damp ground, planks, etc.

[1] *l. c.* D.

Entomophthora curvispora, Nowakowski *l. c.* **A**; *l. c.* **B**, p. 163, figs. 68–70. Sorokin *l. c.* **C**, p. 233.

Under this name Nowakowski has described a form peculiar for its strongly curved conidia, which are elongate, rounded at both extremities and measure 10–15μ × 25–40μ. They resemble the curved forms occurring in *E. variabilis*, but are broader and more rounded basally and much larger. The secondary conidia are represented as perfectly spherical. The resting spores are true zygospores produced by a *Spirogyra*-like conjugation; and of the usual form. The species is parasitic upon *Simulia latipes*, a small fly.

Tarichium megaspermum, Cohn *l. c.* **B**. Sorokin, *l. c.* **C**, p. 235, figs. 600-602, 598, 599, 635–636. Schroeter *l. c.*, p. 223.

This species is known only from its resting spores, which have been thoroughly described and figured by Cohn, and is parasitic upon the larvae of *Agrotis segetum* which are turned black by the disease. The resting spores are apparently azygospores borne laterally or terminally from hyphae and are peculiar on account of their dark brown epispore which is marked by sinuous furrows. The epispore is also frequently opaque showing no furrows. The spores are spherical and of large size measuring from 34μ to 55μ, average 50μ. The figures given by Sorokin are copied from Cohn's plates and the species has not, I believe, been noticed since its original description. It should be noted that *E. virescens* occurs in America on a similar host and may prove to be identical with this species.

Entomophthora Phryganeae, Sorokin *l. c.* **C**, 239, figs. 578, 628 *a, b*.

Sorokin figures as characteristic of this species a long clavate body with a rhizoid-like basal portion and a terminal round spore with a prominent rather narrow base of attachment. In his text he states that the fungus was found on *Phryganea grandis* (June 26, 1881), growing only on the lower surface (between the first and second pair of legs as indicated in the figure) being wholly superficial and not appearing within the body of the host. The hyphae consist of two portions separated by a septum. The conidia are round 8×6–7μ, the hyphae being 5μ in breadth. The rhizoid-like basal expansion (by which the hypha is apparently attached) is said to be characteristic. It is scarcely necessary to remark that this can hardly be an *Empusa* and its position even among the Entomophthoreae seems very doubtful.

Sorokin remarks concerning this and the succeeding form, that he cannot vouch for their distinctness from lack of material.

Entomophthora pelliculosa, Sorokin *l. c.* **C**, p. 240, fig. 629.

Under this name Sorokin describes an *Empusa* found on a "flower fly," *Anthomyia pagana*.

"The parasite resembles the ordinary *E. Muscae*, but the discharged conidia have the strange peculiarity of being covered with several layers concentrically distributed, as if a drop of protoplasm discharged simultaneously with the conidia had dried at several different intervals forming each time something in the shape of an envelope. This characteristic is so constant that all the conidia scattered along the substratum were surrounded by sharply defined concentric lines." The figure represents a spore of the *Grylli* type which bears little resemblance to that of *E. Muscae*, so that any determination based upon the figure and description is not possible.

Tarichia uvella, Krassilstchik *l. c.*, p. 95.

Under this name Krassilstchik has described a fungus, growing in coleopterous larvae, which is characterized by the production of a mass of brick-red "*Tarichium*" spores produced by a process not observed, and cohering in small, grape-like clusters as indicated by the specific name. The spores are described as round, papillate, 8–10μ in diameter, surrounded by a wall of no great thickness. In a nutritive fluid they germinated in four days, producing septate hyphae which after a week grew out of the culture fluid and produced single, terminal, cylindrical, colorless spores, $9 \times 3\mu$.

This does not appear to be an *Empusa* from the course of development described, although it might possibly be related to *Massospora*. Concerning this, it is, however, impossible to judge without figures or more detailed information concerning the species.[1]

Massospora Peck.

Massospora cicadina, Peck *l. c.*, p. 44. Leidy, Proc. Acad. Nat. Sci., Phil. Vol. x, p. 235 (no name).

Conidia(?) produced from short hyphae or hyphal bodies, *within* the host; nearly spherical to ovoid, tapering towards a small basal papilla of attachment; smooth or papillate-verrucose, $10 \times 18\mu$–$18 \times 25\mu$, forming a yellowish mass in the abdominal cavity exposed as a coherent mass by the falling away of the abdominal rings. *Resting spores* (?) spherical, roughly reticulated, slightly colored, 38–50μ in diameter (Peck). Host not attached to substratum.

Hosts. Hemiptera: larvae, pupae and imagines of *Cicada septendecem*.

Habitat. New York, New Jersey, Washington, D. C., Illinois, Michigan, Texas.

This singular form should, I think, undoubtedly be placed among the *Entomophthoreae*, although it is decidedly anomalous in some respects. Professor Peck is inclined to place it near *Protomyces* among the Coniomycetes; owing perhaps to the fact that the origin of the spore mass from the characteristic entomophthoroid bodies (figs. 415–419) was not apparent in the types. Whether these spores which fill the whole abdominal cavity are morphologically similar to the conidia of Empusae, or are a kind of azygospore or chlamydospore I am unable to say, having examined only dried material in which it was, of course, impossible to discover the exact process of formation and separation. Their general appearance is certainly that of conidia; yet, unless a columella can be demonstrated in connection with their formation they must be regarded as of a different

[1] *Entomophthora Anisopliae* of Metschnikoff (Zeitschr. d. Kaiserl. Landwirth, Gesell. f. Neurussland, Odessa, 1879, pp. 21–50, with plate), which attacks coleopterous larvae, is perhaps an Isaria, the spores measuring $4.8 \times 1.6\mu$. It is placed by Sorokin (*l. c.* C, p. 268) as belonging to a genus of Basidiomycetes which he calls *Metarhizium*. The names *E. macrospora* (De Bary Vergl. Morphol. d. Pilze) and *E. muscarina* (Comptes Rendus, Vol. 89, p. 750) are apparently printers' errors.

nature. Of these spores there are two kinds usually to be seen in preparations: a larger form nearly resembling an *Empusa* conidium and possessing a perfectly smooth outer wall (figs. 421–423); and a second form, thicker walled, smaller, distinctly papillate in most instances, but produced similarly from hyphal bodies (figs. 424–428). The development of these spores after formation is wholly unknown, although there can be little doubt that they furnish the immediate means of spreading the disease. It should be noted that the anterior portion of the host's body is wholly free from fungus in the specimens which I have examined. The host may thus live for a considerable time after the abdominal rings have begun to fall away and in this manner disseminate the spores by its own movements. That this is the fact seems certain from the observations of Professor French, who writes me that he has seen both larvae and imagos of the locust moving about at Carbondale, Ill., in the condition just described. The probable development of the spores after falling from the host may be inferred from analogy with Empusae generally, and would naturally consist in the production of secondary conidia discharged as in Empusae, and affording the direct means of infection. The smaller type of spore from the considerable thickness of its walls is manifestly adapted to await uninjured the occurrence of conditions favorable to its germination and the hypothetical course of development given above would thus result in a dissemination perhaps quite as effectual as in the usual course adopted by Empusae.

I have included as "resting spores" a second type of spore described by Peck as occurring in certain individuals, although never having seen these spores I am unable to determine whether I am right in so doing. The description quoted gives no note of either their shape or origin, so that I am only justified in considering them resting spores from their analogy to similar spores in *Empusa*.

The distribution of the species is apparently wide, and a further study of the facts connected with its history and development should be full of interest. Whether the fungus is adapted to a subterranean existence, attacking the larvae during their seventeen years of existence and thus appearing subsequently on the fully developed host, or whether it is continued for this long period by resting spores (a supposition highly improbable), or by the infection of isolated specimens of the same or nearly allied hosts which continue the infection during this period, is quite uncertain. It is apparently liable to appear wherever the *Cicada* is known, as shown by the localities above mentioned. I am indebted to the kindness of Mr. L. O. Howard for specimens received from Michigan which, together with an example in Dr. Farlow's herbarium from Texas are the only specimens which I have examined.[1]

BASIDIOBOLUS Eidam (1885).

Basidiobolus Ranarum, Eidam *l. c.* Schroeter *l. c.*, p. 224.

Conidia nearly spherical to subovoid, tapering slightly to a rounded base from which the small sharply pointed papilla of attachment projects abruptly. Average measurements

[1] The above was in press before the author had seen the excellent summary of contagious insect diseases by Prof. S. A. Forbes (Psyche, Vol. V, pp. 3–12, Cambridge (1888)), in which he places the present genus among the Entomophthoreae.

$37 \times 40\mu$–$40 \times 45\mu$. *Conidiophores* arising from single cells of hyphae, simple, much swollen terminally, this swelling developing into a peculiar piece, the basidium, which is discharged with the spore. *Secondary conidia* like the primary, sometimes produced on a capillary conidiophore. *Resting spores*, zygospores, spherical, with an irregularly pitted or folded epispore; 25–45μ in diameter; pale orange yellow or nearly colorless, sometimes opaque from a dark brown incrustation of the epispore; produced by the conjugation of two adjacent cells of a hypha, or of two conidial spores, through the absorption of the intervening cross partition; the union being preceded by the appearance of two finger-like projections, one from either cell, which are applied to one another and, becoming septate near their tips, persist as appendages to the mature spore.

On the excrement of frogs.

Habitat. Cambridge, Mass.; Europe.

Beyond the hitherto unrecorded occurrence, in America, of this most interesting form, I have nothing new to add to the admirable monograph of Eidam above cited. The fungus appeared on the excrement of frogs kept in the biological laboratory at Cambridge for purposes of dissection, and was obtained by filtering the water in which the frogs were kept and placing the sediment in a tin box. I was unable at the time to make artificial cultivations of the spores, by means of which the studies of Eidam were carried out, and the figures given on plate 21 are derived from specimens growing on the natural substratum of the fungus. It is probably for this reason that the production of zygospores seems to vary slightly from that described by Eidam, in that they appear to be formed near the branched extremities of very large and sparingly septate hyphae. The early stages of the process I did not observe, and for a complete morphological history of the species the beautiful plates of Eidam should be consulted.

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American.

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European.

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DESCRIPTIONS OF THE PLATES.

*** The following figures are, with the exception of those representing host insects, from camera drawings slightly reduced by photography and done on stone from the negatives. Figures marked with an asterisk were magnified 230 diameters approximately in the original drawings; and the remainder, with the exception of the host insects, were magnified 435 diameters approximately.

PLATE 14.

Empusa Muscae, figs. 1–9.

*Fig. 1. Group of conidiophores showing conidia in several stages of development.
Fig. 2. Basidium after the discharge of the conidium.
Fig. 3. Basidium bearing conidium before discharge.
Fig. 4. Hyphal body germinating within the host.
Figs. 5–6. Conidial spores discharged upon a slide and surrounded by a mass of protoplasm from the basidium.
Figs. 7–8. Secondary conidia of the second type (unlike the primary).
Fig. 9. Secondary conidium of the second type before discharge from the primary conidium.

Empusa Culicis, figs. 10–16.

Fig. 10. Group of conidiophores.
Figs. 11–12. Primary conidia two of which are surrounded by a mass of protoplasm, the two others (*a a*) being free.
Fig. 13. Secondary conidium of the second type before discharge from the primary conidium.
Fig. 14. Secondary conidium of the second type.
Fig. 15. Two chlamydospores formed within the host.
*Fig. 16. A rhizoid formed by the adhesion of two filaments.

Empusa Grylli, figs. 17–48.

*Fig. 17. Group of conidiophores of different ages which have separated themselves from the empty hyphae left behind, by successive cross partitions.
*Fig. 18. Conidium before discharge from the basidium.
*Fig. 19. Upper part of basidium after discharge of the conidium showing the columella as a rounded prominence.
*Fig. 20. Primary conidium producing a secondary conidium of the usual type.
Figs. 21–24. Conidia from grasshopper (Acridian).
Figs. 25–28. Conidia from hairy caterpillar (Arctian).
Figs. 29–30. Conidia from wood cricket (*Ceuthophilus*).
*Figs. 31–35. Successive stages in the formation of resting spores by a possibly sexual process.
*Figs. 36–39. Variations in the process of forming resting spores by the method figured in figs. 31–35.
*Fig. 40. Production of a terminal resting spore asexually from a culture of chlamydospores taken from a caterpillar and made to develop in water upon a slide.
*Fig. 41. A resting spore of irregular shape formed by incomplete budding from a hypha.
*Fig. 42. A resting spore produced within a hyphal body.
*Fig. 43. A resting spore in process of budding from a hyphal body.
*Fig. 44. A mature resting spore.
*Fig. 45. Two septate hyphae taken from the femur of an Acridian, showing a point of anastomosis and numerous small outgrowths together with the lateral production of a resting spore.
*Fig. 46. A chlamydospore germinating.
Fig. 47. A resting spore rendered double by the imperfect union of the two divisions of a hyphal body.
Fig. 48. An Acridian attacked by *E. Grylli*, after remaining a few hours in a moist chamber.

PLATE 15.

Empusa Tenthredinis, figs. 49–55.

Fig. 49. Secondary conidium in process of formation from a primary spore.
Figs. 50–55. Primary conidia from a species of *Tenthredo*.

Empusa conglomerata? figs. 56–62.

Figs. 56–59. Primary conidia from larvæ of *Tipula* sp.
Figs. 60–61. Resting spores in process of formation by budding from hyphal bodies nearly spherical in shape, from the same host.
Fig. 62. Mature resting spore.

Empusa apiculata n. s., figs. 63–75.

*Fig. 63. Conidiophores tending to become digitate. From small fly.
*Fig. 64. Simple conidiophore arising directly from a rounded hyphal body. From small fly.
Fig. 65. A primary conidium germinating and producing a secondary conidium. From small fly.
Figs. 66–68. Primary conidium from small fly.
Fig. 69. Conidium from deltoid moth.
Fig. 70. Conidium from caterpillar of *Hyphantria.*
Figs. 71–73. (*Var. Major*), primary conidia from beetle (*Ptilodactyla serricollis*).
*Fig. 74. Resting spore in process of formation from short hyphae here associated with a cross partition. From Geometrid moth.
*Fig. 75. Terminal portion of a rhizoid from small fly.

Empusa Planchoniana ? figs. 76–81.

Figs. 76–78. Primary conidia from aphides, fig. 77 having a slight apiculus.
Figs. 79–81. Resting spores forming interstitially and terminally from hyphae.

Empusa papillata n. s., figs. 82–90.

*Fig. 82. Conidiophores.
Fig. 83. Secondary conidium in process of development from a primary spore. The columella is forced into the secondary spore probably in this case by the contraction of its contents, the primary spore being empty.
Fig. 84. Terminal portion of a rhizoid.
Figs. 85–89. Primary conidia.
Fig. 90. A mature resting spore.

PLATE 16.

Empusa Caroliniana n. s., figs. 91–105.

*Fig. 91. Conidiophores, one arising directly from a hyphal body.
Fig. 92. A hypha the contents of which have become contracted into hyphal bodies.
Figs. 93–94. Primary conidia from fresh material.
Figs. 95–103. Primary conidia as they appear in dried material.
Fig. 104. Secondary conidium in process of formation from a primary spore.
Fig. 105. A mature resting spore. All these figures are from *Tipula* sp.

Empusa (Triplosporium) Fresenii (figs. 106–140).

*Figs. 106–108. Masses of nearly naked protoplasm from which the hyphal bodies (fig. 127) are formed.
Fig. 109. Conidium before discharge from the basidium.
Fig. 110. Conidium germinating in the ordinary way.
Figs. 111–116. Primary conidia.
Fig. 117. A secondary conidium of the second type produced from a primary conidium, on its capillary conidiophore.
Fig. 118. A secondary conidium of the second type produced from a conidiophore which is neither capillary nor of the usual type.
Fig. 119. A secondary conidium of the second type, borne on a capillary conidiophore, which has begun to germinate before separating from it.
Fig. 120. A secondary conidium of the second type germinating laterally by a capillary conidiophore.
Figs. 121–122. Secondary conidia of the second type germinating from their apices in the usual manner.
Figs. 123–124. Secondary conidia of the second type.
Fig. 124. A primary conidiophore producing three capillary conidiophores, the middle one beginning to swell into a spore.
Fig. 125. A hypha of germination of the usual type, from a primary conidium, has sent up a capillary conidiophore at the tip of which a secondary conidium of the second type is beginning to form.
Fig. 126. A hyphal body germinating to form a conidiophore.
Fig. 127. Two hyphal bodies taken from a mass filling the abdomen of *Aphis.*
Figs. 128–140. Two hyphal bodies lying side by side previous to conjugation begin to show slight prominences on their upper inner sides.
Fig. 129. These prominences have become gametes which have come in contact with one another midway between the two hyphal bodies.
Fig. 130. The partition wall between the gametes has wholly or partially disappeared and a bud has begun to appear rising upwards from their point of union.

Figs. 131–134. Showing this bud in several successive stages of development.
Figs. 135–136. The bud has become the mother cell of a zygospore while the two hyphal bodies remain attached as bladders which contain certain fatty bodies.
Fig. 137. A mature zygospore lying free in its mother cell, the walls having been separated through the absorption of water.
Fig. 138. A small zygospore to which the ragged remnants of the hyphal bodies are still attached as in the previous figure.
Figs. 139–140. Zygospores from which the remnants of the hyphal bodies have wholly disappeared, a remnant of the gametes still adhering to fig. 140.

Empusa (Triplosporium) lageniformis n. s., figs. 141–160.

*Fig. 141. Young conidiophores of a digitate type seldom seen in this species. All the figures are from *Aphides* on white birch (*B. populifolia*).
*Fig. 142. Conidiophores of the usual type.
Fig. 143. A primary conidium of the usual type germinating to produce a secondary conidium of the first type.
Figs. 144–145. Hyphal bodies germinating to form conidiophores.
Figs. 146–154. Primary conidia.
Fig. 155. A primary conidium has produced a capillary conidiophore, the apex of which has begun to swell into a secondary conidium of the second type.
Figs. 156–157. Two primary conidia have produced capillary conidiophores upon which are borne mature secondary conidia of the second type.
Figs. 158–160. Three secondary conidia of the second type in different stages of germination.

PLATE 17.

Empusa (Entomophthora) Lampyridarum n. s., figs. 161–172.

*Fig. 161. Conidiophores of a simple type. The type of the species is however probably compound.
Figs. 162–166. Primary conidia.
Figs. 167–171. Secondary conidia of the second type.
Fig. 168. A secondary conidium of the second type has produced a capillary conidiophore the apex of which is becoming swollen into a tertiary conidium of the same type.
Figs. 169–170. Two primary conidia bearing mature secondary conidia of the second type on capillary conidiophores.
Fig. 172. Appearance of host, *Chauliognathus Pensylvanicus*, attacked by this species.

Empusa (Entomophthora) geometralis n. s., figs. 173–178.

Fig. 173. *Eupithecia* attached to a pine needle by haustoria before death.
Fig. 174. *Thera* similarly attached showing position of conidiophores.
Fig. 175. Group of primary conidia.
Figs. 176–177. Two primary conidia producing secondary conidia of the second type on capillary conidiophores.
Fig. 178. Two secondary conidia of the second type.

Empusa (Entomophthora) occidentalis n. s., figs. 179–199.

*Fig. 179. Rhizoid with irregularly expanded extremity.
*Fig. 180. Digitate conidiophore.
Fig. 181. Basidium and conidium before discharge.
Figs. 182–184. Primary conidia with fat globules.
Figs. 185–189. Primary conidia of the usual appearance. Figs. 183 and 185 are more distinctive of the species.
Fig. 190. Primary conidium which has germinated to produce a secondary conidium of the first type.
Fig. 191. Primary conidium which has produced a capillary conidiophore on which is borne a mature secondary conidium of the second type.
Fig. 192. Primary conidium germinating as in the last figure: the secondary conidium being immature.
Fig. 193. Secondary conidium of the second type.
Fig. 194. Secondary conidium of the second type in process of germination.
Fig. 195. Mature resting spore.
Figs. 196–199. Formation of resting spores by a possible sexual process.

Empusa (Entomophthora) sphaerosperma, figs. 200–219.

Fig. 200. *Colias* attacked by the fungus.
Fig. 201. A small hymenopterous insect similarly attacked.
*Fig. 202. A compound conidiophore.

Fig. 203. Primary conidia from small gnat.
Fig. 204. The same from *Thrips* sp.
Fig. 205. The same from a species of *Musca*.
Fig. 206. The same from an ichneumon.
Fig. 207. The same from *Colias philodice*.
Fig. 208. The same from *Phytonomus* larva.
Fig. 209. The same from rose leaf-hopper (*Typhlocyba*).
Fig. 210. A primary conidium producing a capillary conidiophore on which is borne a mature secondary conidium of the second type.
Fig. 211. The same. The secondary conidium in process of formation.
Fig. 212. A secondary spore of the second type unusually long.
Fig. 213. A secondary conidium of the second type of the usual form.
Figs. 214–216. Resting spores in process of formation from short hyphae, associated with a cross partition in each case.
Fig. 217. Resting spore in process of formation from a single short hypha.
Figs. 218–219. Mature resting spores.

PLATE 18.

Empusa (Entomophthora) Aphidis, figs. 220–240.

*Fig. 220. Compound conidiophore.
*Fig. 221. Cystidium.
Fig. 222. Simple conidiophore: the protoplasm in the basidium has separated itself from the empty hypha below by successive cross partitions.
Figs. 223–236. Primary conidia.
Fig. 237. Two secondary conidia of the second type.
Fig. 238. A primary conidium bearing a secondary conidium of the second type.
*Fig. 239. A hyphal body germinating in all directions.
Fig. 240. A primary spore germinating in water, the protoplasm separating itself by cross partitions from the empty hypha.

Empusa (Entomophthora) dipterigena n. s., figs. 241–250.

Figs. 241–247. Primary conidia from a small fly, figs. 243 and 244 being characteristic of the species.
Fig. 248. Primary conidium bearing a secondary conidium.
*Fig. 249. Rhizoid with terminal expansion. The divisions of the expansion should be more truncate.
Fig. 250. A mature resting spore produced externally.

Empusa (Entomophthora) virescens n. s., figs. 251–261.

Fig. 251. Digitate conidiophore.
Figs. 252–259. Conidia.
Fig. 260. Conidium which has been discharged without the rupture of the mother-cell wall which has merely stretched.
*Fig. 261. Hyphal body germinating in all directions.

Empusa (Entomophthora) Americana n. s., figs. 262–273.

*Fig. 262. A group of rhizoids.
Figs. 263–271. Conidia.
" 272–273. Two mature resting spores; fig. 272 showing separation of the inner and the two outer walls.

Empusa (Entomophthora) montana n. s., figs. 274–285.

*Fig. 274. A digitate conidiophore produced directly from a chlamydospore.
*Fig. 275. Two cystidia.
*Fig. 276. Terminal portion of a rhizoid showing its attachment to a bit of *Sphagnum*.
Fig. 277. Gross appearance of the fungus many times enlarged.
Figs. 278–285. Conidia.

PLATE 19.

Empusa (Entomophthora) echinospora n. s., figs. 286–305.

Figs. 286–294. Conidia.
Fig. 295. Terminal portion of a rhizoid.

Fig. 296. A zygospore which seems to have resulted from a double conjugation.
Fig. 297. A group of sporophores emerging from the host's body previous to the formation of zygospores. One of their number has grown beyond the rest and subsequently forms part of a network which holds the mass of external zygospores.
Figs. 298–299. Two instances of external conjugation.
Fig. 300. Conjugation taking place within the host.
Figs. 301–302. Further examples of external conjugation.
Figs. 303–304. Resting spores formed internally, the process of conjugation not visible.
Fig. 305. Mature resting spore.

Empusa (Entomophthora) sepulchralis n. s., figs. 306–326.

*Fig. 306. A cystidium somewhat immature.
*Fig. 307. The terminal portion of a cystidium at a more advanced stage.
*Fig. 308. A digitate conidiophore arising directly from a spherical hyphal body.
Fig. 309. A hyphal body beginning to germinate.
Figs. 310–317. Primary conidia.
Figs. 318–319. Secondary conidia of the second type.
Fig. 320. Primary conidium in which the mother-cell wall has separated from the spore, remaining attached only at its point of dehiscence from the basidium.
Fig. 321. Primary conidium in which the separation from the mother-cell has become complete.
*Fig. 322. Conjugation of two hyphae and first budding of the zygospore from one of the gametes.
*Figs. 323–325. Several stages in the formation of a zygospore. In fig. 325 the whole contents of the conjugating cells have passed into the zygospore.
Fig. 326. Mature zygospore. (The circles of dots are due to careless engraving).

PLATE 20.

Empusa (Entomophthora) variabilis n. s., figs. 326–345.

*Fig. 327. Compound conidiophore.
*Fig. 328. Rhizoids.
Figs. 329–342. Primary conidia.
Fig. 343. Primary conidia among the first discharged.
Fig. 344. Formation of a secondary conidium of the first type.
Fig. 345. Formation of a secondary conidium of the second type.
Fig. 346. Secondary conidium of second type.

Empusa (Entomophthora) rhizospora n. s., figs. 347–378.

*Fig. 347. Conidiophore arising from spherical hyphal body.
*Fig. 348. Cystidium.
Figs. 349–360. Primary conidia.
Fig. 361. Production of secondary conidium of the first type.
Fig. 362. Production of secondary conidium of the second type.
Figs. 363–365. Secondary conidia of the second type.
Figs. 366–367. Production of "pseudoconidia" from hyphal bodies resulting from the general degeneration of the conidiophores.
Figs. 368–369. Two of the pseudoconidia fully developed.
*Fig. 370. Formation of a zygospore by the conjugation of the free ends of two hyphae.
*Fig. 371. *Spirogyra*-like conjugation resulting in the production of a spore from both gametes.
*Figs. 372–373. Two similar points of conjugation in which the rhizoid-like enveloping processes are developing from the base of the spore.
*Fig. 374. Group of mature zygospores showing indurated hyphae and rhizoid-like processes.
Fig. 375. A single zygospore.
Fig. 376. A zygospore freed from the epispore.
Fig. 377. A "Caddis fly" showing the growth of conidiophores.
Fig. 378. Gross appearance of the zygospores produced externally over the host.

PLATE 21.

Empusa (Entomophthora) gracilis n. s., figs. 379–391.

*Fig. 379. Conidiophore.
Fig. 380. Production of secondary conidium of the first type.

Fig. 381. Secondary conidium of the second type.
Figs. 382–391. Primary conidia.

Empusa (Entomophthora) conica, Nowakowski, figs. 392–408.

*Fig. 392. Conidiophore originating from spherical hyphal body.
Fig. 393. Cystidium.
Figs. 394–402. Primary conidia.
Figs. 403–404. Primary conidia produced in dryer situations.
Fig. 405. Production of secondary conidium of the first type.
Figs. 406–407. Secondary conidia of the second type.
Fig. 408. Production of secondary conidium of the second type.
*Fig. 409. Production of a zygospore by *Spirogyra*-like conjugation.

Basidiobolus Ranarum, Eidam, figs. 140–144.

Fig. 410. Conidiophore with conidium budding from its apex.
Fig. 411. Conidium still connected with the basidium.
Fig. 412. The basidium (*a*) separated from the conidium.
Figs. 413–414. Zygospores in different stages of development with the "nabel" (*a*,*a*), persistent.

Massospora cicadina, Peck, figs. 415–429.

Figs. 415–417. Hyphal bodies.
Figs. 418–420. Production of spores from hyphal bodies.
Figs. 421–423. Spores of the larger and smooth type.
Figs. 424–428. Spores of the usual type.
Fig. 429. One of the same spores seen in optical section,

Note.—The present investigation was carried on in the Cryptogamic laboratory of Harvard University and was presented as a graduating thesis May 1, 1888.

CONTENTS.

INDEX OF GENERA AND SPECIES.

INDEX OF HOST-INSECTS.

ERRATA.

Page 142, line 11 and p. 143, line 6; for *apiculatus* read *apiculata*.
Page 153, line 11, after *conica* insert *radicans*.
Page 141, 3d line from bottom, for condition read — conditions.
Page 150, lines 6 and 9 and p. 174, line 26, for Krasilstchik read — Krassilstchik.
Page 166, line 10, after separation insert — is.
Page 190, line 4, for *Tarichia* read — *Tarichium*.
Page 192, line 27, for larvae read — larval.
Page 200, for Metarhigium read — Metarhizium.
Plate xv, for var. apiculata read — apiculata.